Puma space use and dispersal in tropical biodiversity hotspots: bridging a gap to connect individuals to populations

Short title: Puma movement and dispersal in biodiversity hotspots

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Abstract

Assessing residency and dispersal behavior of apex predators and its consequences for landscape connectivity is of paramount importance for understanding population- and ecosystem- effects of anthropogenic land use change. However, basic information on animal space use is still lacking, particularly in the Tropics. Here we synthesize ranging and dispersal ecological information on pumas (*Puma concolor*) and present estimates of space use, dispersal, and movement of pumas in an ecotone between biodiversity hotspots in Southeastern Brazil. Using GPS data for 14 GPS-collared pumas and land use data, we assessed when, how long, and how far individuals dispersed; what factors influenced puma home range size; and how movement patterns changed according to land use and proximity to infrastructure, during residency and dispersal. We present the first detailed record on dispersal of pumas in Brazil, including long-distance dispersals, and show that pumas moved faster and less tortuously during dispersal than during residency. Pumas moved slower and had smaller home ranges in landscapes with higher proportion of forest, pointing to the importance of forests as habitat for pumas. In contrast, movement rates were higher in open pastures, mainly during dispersal and nighttime. Our study underscores the scarcity of research on puma space use and dispersal in South America and reveals divergences in dispersal behaviors compared to North America, especially concerning dispersal ages. We call for more comprehensive studies on movement ecology of carnivores combined with long-term population monitoring, to allow linking individual behavior with metapopulation dynamics and landscape connectivity and drawing more effective measures to sustain their populations.

Key-words: habitat fragmentation, movement ecology, home range, residency, Atlantic Forest, Cerrado, *Puma concolor*

1 Introduction

Space use is a crucial aspect of animal behavioral ecology and is shaped by interactions among conspecifics, heterospecifics, and the environment (Nathan et al., 2008). Understanding wildlife movement and space use is pivotal not only for deciphering the dynamics of species' interactions but also for devising conservation and management strategies in human-modified landscapes. Animal home ranges and movement patterns serve as indicators of a species' spatial and resource needs (Börger, Dalziel, & Fryxell, 2008). However, a comprehensive understanding of population dynamics and connectivity requires knowledge on dispersal – the movement of individuals or propagules across population, with consequences for gene flow, what includes natal and breeding dispersal (Ronce, 2007). Despite being fundamental aspects of wildlife ecology, home range and dispersal remain unknown for a wide range of species and regions, as in Central and South America (Gonzalez-Borrajo, López-Bao, & Palomares, 2017; Oliveira et al., 2021). This knowledge gap, associated with the accelerated habitat loss, leads to the need to make predictions and transferring models based on data collected elsewhere, typically in highly studied areas in the Global North (e.g. Castilho et al., 2011; Crooks et al., 2011). Since the quality and validity of these transferred models is hardly evaluated (Yates et al., 2018), much remains unknown about the movement and its population consequences in understudied regions, potentially resulting in ineffective or suboptimal conservation policies.

Large carnivores have been shown to use different resources and habitats (Magioli et al., 2014, 2019) and move smaller distances (Tucker et al., 2018) in human-modified landscapes. As a consequence, these carnivores have less access to high-quality habitat and decreased connectivity between populations (Crooks et al., 2011), which typically results in diminished genetic variability (Lino et al., 2019; de Almeida-Rocha et al., 2020) and lower population densities (IPBES, 2019; J. J. Thompson et al., 2021). Fragmentation and declines in carnivore populations can have cascading effects on communities and ecosystems, particularly among top predators (Ritchie & Johnson, 2009; Kuijper et al., 2016; LaBarge et al., 2022). Therefore, understanding residency, dispersal behavior, and landscape connectivity is crucial for apex predators.

Pumas (*Puma concolor*) are the top predators with the broadest geographical distribution in the Americas, occurring from Canada to the Southern tip of the Andes (Sunquist & Sunquist, 2002), and their presence has profound community and ecosystem consequences (LaBarge et al., 2022). While the species is globally categorized as of least concern for conservation (Nielsen et al., 2015), within Brazil it is considered as vulnerable in several states (BRASIL, 2022). Despite extensive studies on puma space use and population dynamics in North America (Hemker, Lindzey, & Ackerman, 1984; e.g. Beier, 1995; López-González & González-Romero, 1998; Maehr et al., 2002; Zeller et al., 2017), their ecology remains relatively unknown in other regions. In Brazil, the first puma studies occurred in projects where they occurred in sympatry with jaguars (*Panthera onca*) (Gonzalez-Borrajo, López-Bao, & Palomares, 2017 and references therein). More recently, new studies have been unveiling aspects of habitat use (Lyra-Jorge et al., 2010; Azevedo et al., 2021), diet (Magioli et al., 2014; Magioli & Ferraz, 2021), landscape genetics (Castilho et al., 2011; Miotto et al., 2011, 2014), and reintroduction of individuals in nature (Paula et al., 2015; Adania et al., 2017), yet knowledge regarding movement and dispersal remains scarce. Unlike the Northern Hemisphere, few studies in the Southern hemisphere provide detailed descriptions of puma movement and resource selection based on GPS data (Azevedo et al., 2018, 2021), with just one documented case of (long-distance) dispersal in Patagonia (Elbroch et al., 2009). Consequently, critical gaps persist in our understanding of puma ecology, including residency and dispersal behavior, the determinants of these patterns (Stoner et al., 2013), and their implications for (meta)population dynamics (Sweanor, Logan, & Hornocker, 2000).

In North America, 50 to 75% of puma deaths result from human persecution or direct human actions (Weaver, Paquet, & Ruggiero, 1996; Sunquist & Sunquist, 2002), and a similar scenario is expected across their distribution (Zanin, Palomares, & Brito, 2015). On the one hand, large-scale agricultural expansion, livestock, urbanization, and industrial development have been encroaching on natural areas, leading to habitat loss and fragmentation (Gonzalez-Borrajo, López-Bao, & Palomares, 2017; Souza et al., 2020). These changes are expected to lead to increasingly isolated puma populations. On the other hand, the wide variability in puma habitat use, diet, and behavior distinguish them from jaguars and other small cats (Magioli et al., 2014; Gonzalez-Borrajo, López-Bao, & Palomares, 2017) and might grant them resilience against landscape changes. Research in Southern and Southeastern Brazil reported absence of genetic structure in the studied puma populations (Castilho et al., 2011; Miotto et al., 2011), suggesting non-isolated populations (but see Saranholi, Chávez-Congrains, & Galetti, 2017 for an opposite conclusion). However, one of the studies (Castilho et al., 2011) adapted an approach and data from North America based on expert knowledge (LaRue & Nielsen, 2008), and uncertainties persist regarding the applicability of such approaches to the South American context.

We investigated the dispersal, home range, and movement patterns of pumas in fragmented landscapes of Southeastern Brazil and compared them with published information from other regions. Using GPS data, we characterized puma dispersal in highly fragmented landscapes, estimated residency areas and home range sizes, and investigated the landscape factors which determine home range size and movement patterns during both residency and dispersal. We formulated hypotheses for each of these aims. First, we expected pumas to move faster and more directionally during dispersal (Barry et al., 2020), if compared to residency [*fast dispersal* hypothesis]. Second, we expected pumas to present smaller home ranges in areas with higher proportion of forest and close to rivers (Azevedo et al., 2021; J. J. Thompson et al., 2021), assuming forests and water would provide them abundance of prey resources [*forest importance* hypothesis]. An alternative hypothesis regarding home range areas would be that, given the wide puma behavioral plasticity and the documented consumption of alternative prey from agricultural matrices in fragmented landscapes (Magioli et al., 2014), pumas do not increase their home ranges in landscapes with less forest amount [*behavioral plasticity* hypothesis]. Third, we expected pumas to use forests less frequently and cross agricultural and anthropogenic areas faster and more often at night, when there is less human disturbance (Morrison, Boyce, & Nielsen, 2015), especially during dispersal events [*human disturbance* hypothesis].

2 Materials and Methods

2.1 Study area

The study was conducted in the ecotone between two biodiversity hotspots, Atlantic Forest and Cerrado, in the state of São Paulo, Brazil. The Atlantic Forest, one of worlds' most biodiverse yet fragmented biomes, retains only about 23% of its original forests (Vancine et al., 2023). The Brazilian Cerrado, the largest Savannah in the Americas and the richest in species worldwide, currently has only 50% of its native vegetation (Project MapBiomas, 2020), despite harboring approximately 30% of Brazil's biodiversity. In São Paulo, the Atlantic Forest consists of a few large patches of subtropical moist rainforest close to the coast and thousands of small deciduous and semi-deciduous forest patches in the countryside (Vancine et al., 2023). The Cerrado in São Paulo is composed of a combination of semi-deciduous forests and savannahs.

Most pumas were captured and monitored along the Tietê River basin, covering the region between the cities of Promissão, Ibitinga and Barra Bonita (21°46'04'' S, 48°59'07'' W; Fig. 1). The area is predominantly characterized by anthropogenic land use, including sugarcane plantations, pasture lands for cattle production, citrus plantations, and other anthropic uses. Forests cover only 13% of the region (Project MapBiomas, 2020). Although urban areas occupy merely 3% of São Paulo, they are home to approximately 44 million people, and the state is traversed by dozens of large and small roads. Additionally, one individual was monitored in the Serra do Mar, a mountainous region located in the largest Atlantic Forest continuum along the Brazilian coast (Fig. 1).

Jaguars coexist with pumas in the continuous coastal forests of the Atlantic Forest, but they were already extirpated from the fragmented landscapes towards the interior part of the state, where pumas remain as the sole top predator. In the fragmented areas, pumas primarily prey on nine-banded armadillos (*Dasypus novemcinctus*), capybaras (*Hydrochoeris hydrochaeris*), lowland pacas (*Cuniculus paca*), deer (*Subulo gouazoubira or Mazama* sp.), wild boars (*Sus scrofa*), and several small mammals and birds. Occasionally, pumas also prey on domesticated animals such as lambs and cattle calves.

2.2 Puma GPS data

Pumas were captured with foot snares (Araujo et al., 2020) and collared with GPS collars with a drop-off system (Sirtrack, New Zealand, model Pinnacle). Snares were attached to 7-mm steel cables with swivels at both ends to prevent cable twisting during animals' attempts to scape. Springs were attached to the handle to help absorb the impact from the pumas trying to pull their feet from the snares. The cables were firmly anchored to the ground by four 1-meter-long iron stakes, placed crosswise to ensure a secure anchorage. Trigger tension was set so that it was activated only by large animals (> 20 kg). Snares were set on trails, at locations where pumas had been previously recorded by camera traps or footprint tracks. Blind sets were used without the use of baits. Snares were closed daily in the morning, during visual checks of the sets, and reopened late in the afternoon. To minimize the time animals remained trapped, at night snares were continuously monitored by TBT-500 transmitters (Telonics, Mesa, USA), which indicated if a snare was triggered.

Captured pumas were immobilized with a combination of tiletamine and zolazepam (10mg/kg, Fort Dodge do Brasil), with ketamine supplementation when necessary. After examination, measurement, weighting, and sexing, individual's age was estimated based on the presence of milk or permanent dentition, tooth staining and wear, and other indicative signs (Ashman et al., 1983; Gay & Best, 1996). Temperature, pulse, and breathing of the pumas were monitored throughout the procedure, until complete recovery from anesthesia.

Pumas were fitted with GPS collars and released at the capture location. Some animals captured within urban areas were opportunistically collared and translocated to high-quality forest patches within the same municipality limits. GPS collars recorded one position per hour and positions were daily transmitted through Satellite to a centralized system. Animals were monitored until death (n = 6), collar failure (n = 7), or collar the drop-off (n = 1).

2.3 Environmental data

We compiled environmental data to understand animal movement patterns during dispersal and residency. We used land cover data from the Brazilian Foundation for Sustainable Development (FBDS, 2017), complemented by maps on sugarcane plantations from CanaSat (Rudorff et al., 2010) and pastures for cattle production (Parente et al., 2017). The final land cover map included eight classes: forest, non-forest natural areas, urban areas, forestry, water, sugarcane, pasture, and other anthropic uses. Geographical information on the main roads was obtained from the National Department of Transport Infrastructure (DNIT, 2013). Distance to and density of water, roads, and urban areas was computed to assess their impact on puma movement patterns. Detailed information on these geographical layers is provided in Appendix A. All data processing was conducted using GRASS GIS software, version 7.8 (GRASS Development Team, 2020).

2.4 Identifying and characterizing residency and dispersal

Our analysis centers on differentiating residency and dispersal behaviors. As we considered here, residency is a central-place behavior that defines a home range for the individuals, where they remain for an extended period. As such, residency is composed of movements constrained by the presence of a central attractor. In contrast, dispersal entails spatially unconstrained movements after or before settling in a residency. To identify the transitions between the residency and dispersal behavioral phases (departure and settling events), we followed the approach by Barry et al. (2020) to fit statistical models to each of the residency and dispersal behaviors and test for the most likely dates of transition between them by calculating and maximizing a joint likelihood function for the two models. We employed an Ornstein-Uhlenbeck-Fleming (OUF) model to represent residency, characterized by autocorrelation in locations and speed and by a home range area of use (Fleming et al., 2014; Calabrese, Fleming, & Gurarie, 2016), and a continuous velocity model (CVM) to represent dispersal, defined by a mean value and autocorrelation on speed (Gurarie et al., 2017). For regularly sampled data, the OUF and CVM models may be approximated by autoregressive time series models (an ARMA(1,1) and an ARIMA(1,1,0), respectively; Barry et al., 2020). To avoid sampling gaps, data were resampled to one position per day, which was enough to identify the transitions since dispersal events occur on a time scales longer than a few hours. ARIMA models were fitted separately to x and y coordinates of the movement data, with the same transition dates between behaviors, but a single likelihood function was built for them. For more details, see Barry et al. (2020). To keep the approach simple, and after a qualitative evaluation of the movement of pumas, we did not fit models including more than one dispersal phase and intermediate temporary ranges. We used AIC to evaluate if it was more likely that an individual was resident or disperser. Dispersers were further assessed for evidence of one or two residency phases. Once identified, movement phases were classified into pre- and post-dispersal (both considered as residency) and dispersal.

After movement phases were identified, we calculated the duration of the dispersal events and the Euclidean and total dispersal distances. Euclidean distance was computed as the straight-line distance between the first and last location of the dispersal phase, while the total dispersal distance was the sum of the length of all 1h-steps traveled during dispersal. We also estimated dispersal ages and recorded individuals' fates. We characterized movement patterns in each behavioral phase by fitting a Gamma distribution to the movement rates and a von Mises distribution to the turning angles, including individuals as a random intercept.

To characterize home ranges, we computed variograms and estimated continuous-time movement models and home ranges using the *ctmm* package (Calabrese, Fleming, & Gurarie, 2016; Fleming & Calabrese, 2017a). We fitted three movement models to the residency data: 1) an independent identically distributed process (IID), which although is not a typical movement model is characterized by a home range behavior; 2) an Ornstein-Uhlenbeck (OU) model, which assumes autocorrelation in positions but not in velocities; and 3) an OUF model, as explained above. We fitted movement models through a maximum likelihood approach and used starting values taken from the analysis of variograms. Models were compared through Akaike information criterium adjusted for small samples (AICc). The most likely movement model was used to estimate home range areas using autocorrelated kernel density estimation (AKDE; Fleming et al., 2015; Fleming & Calabrese, 2017b). Even though barriers were not formally included in the computation of the home ranges, when the ranges included large parts of a hydropower reservoir, the 95% AKDE were manually edited to remove the parts within the reservoir limits.

2.5 Effects of the landscape on ranging and dispersal

To understand the effects of landscape on home range size, we fitted generalized linear models with Gamma response and logarithmic link, using the size of the 95% AKDE isopleths as the response variable and the proportion of different land use classes, average road density, and average distance to urban areas within the AKDE as covariates.

To understand the effects of landscape and infrastructure on puma movement, we tested for the influence of land use and the proximity to roads, water, and urban areas on movement patterns. First, a descriptive analysis was made by quantifying the proportion of positions on each land use class on the three behavioral phases – pre-dispersal, dispersal, and post-dispersal ranging. Second, we used a discrete representation of movement, characterized by steps between pairs of positions, to assess the effect of the landscape covariates on movement rates during residency and dispersal. We extracted the landscape information at the beginning of each 1h step and fitted generalized linear mixed models with Gamma response, with movement rate (= step length for hourly displacements) as the response variable and explanatory variables including land use, distance to urban areas, roads, and water, considering the interaction between these covariates, time of day, movement phase. Time of day was included as a binary variable, to account for different behaviors during day and night. Further methodological details are available in Appendix B.

2.6 Literature review

To put our results into context, we conducted a non-systematic review of studies reporting puma dispersal and home range. We searched on Google Scholar for studies including *dispersal* AND *puma* or several of the popular names of pumas, in English (e.g. cougar, mountain lion), Spanish (e.g. león de montaña), and Portuguese (e.g. onça parda, suçuarana) from 1980 to 2019. Additionally, we searched for recent reviews of spatial ecology of pumas and large felids and the references therein. The studies were filtered to keep only research that focused on dispersal (including identifying or comparing dispersal phases, distances, or ages) and possibly other aspects of puma spatial ecology, like home ranges, habitat selection, population or metapopulation dynamics. For each selected study, we recorded dispersal age, fate after dispersal, monitoring method (e.g. VHF, GPS), method to estimate the dispersal phase, and dispersal distance (Euclidean and total dispersal distance), both for each individual (when reported) or averages, standard deviations, and minimum/maximum values for the set of monitored individuals. Using this data, we made a comparison of dispersal ages and distances between the literature and our study.

3 Results

3.1 Pumas in Southeastern Brazil

Between 2015 and 2020, we captured and collared 14 pumas (Fig. 1), of which three were females (21%) and eleven were males (79%). Individuals were monitored on average per 220 days (range = [93, 408] days, n = 14; Table D1), yielding a total of 57,077 positions, with an average of 4,077 per individual (range = [1,642; 8,044], n = 14). Six individuals (3 F, 3 M) maintained residency throughout the monitoring, while the remaining eight, all males, dispersed (Table D1; Fig. D1). Notably, five individuals were translocated before release, four from urban areas to nearby forest fragments, and one individual that was not healthy when captured was kept in captivity for 8 months before translocation (Table D1).

Of the dispersing males, one dispersed immediately when it was released, four started their dispersal within 2 weeks from release, and the last three began dispersal 50, 55, and 88 days after they were collared (Table D2). Average dispersal age was 33 months (range = [22, 43.8] months, n = 8). Dispersal events lasted on average 50 days (range = [11, 140] days, n = 8). Male pumas dispersed a linear median distance of 68.0 km (range = [18.7, 174] km, n = 8), even though the total distance traveled during the dispersal period was much higher, on average 288.3 km (range = [50.6, 524.9] km, n = 7).

Pumas moved faster during dispersal (mean movement rate = 3.67 [95% confidence interval CI = 0.56-24.08] km/day) than during post- (mean = 2.35 [95% CI = 0.36-15.35] km/day) and pre-dispersal residency phases (mean = 1.64 [95% CI = 0.25-10.75] km/day) (Fig. 2). They also exhibited more directional movement during dispersal, with a mean direction closer to zero and less variation in turning angles (von Mises mean = 0.31 [95% CI = -0.08 - 0.70]), in contrast to post- (mean = -2.95 [95% CI = -0.80 – 4.93]) and pre-dispersal residency (mean = -0.17 [95% CI = -2.90 – 1.97), which exhibited higher mean values and greater variation in turning angles (Fig. 2). However, this pattern varied among animals: dispersal could be characterized by a mixture of longer displacements and/or higher directionality (Figs. D2-D4).

Home range sizes varied from 21.6 km^2 to 565 km^2 (average = 206 km^2, Table D3, Fig. D5). All home ranges were characterized by an OUF model and estimated through AKDE. As expected, home ranges computed through AKDE were larger than those computed through minimum convex polygons (MCP) or traditional KDE (Fig. D5), which were historically used in the literature to quantify home ranges sizes (Morato et al., 2016). Home range sizes decreased with increasing proportion of forest (Fig. 3A, β = -0.5, SE = 0.22, p = 0.049), and there was a small signal of home ranges increasing with road density (Fig. 3B, β = 0.368, SE = 0.197, p = 0.095). Additionally, home range sizes were negatively correlated with the proportion of non-forest natural areas and the distance to urban areas and positively correlated with the proportion of sugarcane and forestry (Table D5). However, the amount of different land use classes covaried, and there was stronger evidence for the effect of forests and roads (Table D4).

Pumas crossed pastures more often and used less forest patches during dispersal at night, if compared to residency and daytime (Fig. 4). However, individual variation was observed, with some pumas exhibiting increased forest use during dispersal compared to residency (e.g. Mineiro, Tupã; Fig. D6). The most parsimonious model for 1-h movement rates included land use, distance to roads, urban areas, and water bodies, all in interaction with time of day and movement phase, along with individual sex. As expected, males moved more (mean = 5.30 [95% CI = 5.10-5.51] km/day) than females (mean = 3.43 [95% CI = 3.21-3.67] km/day), and pumas moved faster at night (mean = 7.47 [95% CI = 7.07-7.89] km/day) than during the day (mean = 2.43 [95% CI = 2.28-2.60] km/day). Pumas moved faster in pastures, mainly at night and during dispersal, and more slowly during dispersal in areas of Cerrado (non-forest natural vegetation) and in sugarcane plantations, mainly during the day (Fig. 5A). Pumas also moved more slowly in forests during dispersal and daytime. Pumas exhibited faster movement around 1 km of roads during residency in the daytime, but this effect was absent during dispersal and nighttime (Fig. 5B). Similarly, pumas moved faster around 1 km of urban areas during dispersal at night, but not during residency or in daytime, most likely because they only approached urban areas during dispersal nights (Fig. 5C).

3.2 Literature review

We gathered dispersal data from 24 studies (Appendix C), 23 of which were conducted in North America (95.8%). Earlier studies (pre-2000) primarily used VHF telemetry or capture-recapture methods (n = 17, 70.8%), while GPS collars gained prominence after 2005. Definitions of dispersal differed between studies. Immigration or start of dispersal was often marked by separation from mothers or movement outside the natal range (e.g. Beier, 1995; Stoner et al., 2013), or using the location where animals were released (e.g. Elbroch et al., 2009; D. J. Thompson & Jenks, 2010). Settling or end of dispersal was commonly defined by the individual meeting with an individual of the opposite sex, by a residency or site fidelity to a new range, or by the location of an individual's death (Maehr et al., 2002). These definitions were far from standardized, adapted to the type and resolution of the data, and were omitted in several studies. Measures of dispersal distance also varied, e.g. as the distance between the borders or the centroids of natal and final home ranges or final locations (e.g. López-González, 1999). Apart from 1 study using genetics and 6 studies that did not report the methods to identify dispersal, in all studies (n = 17) the transitions between residency and dispersal were identified visually, with the use of different criteria as the ones mentioned above. In only one study were statistical methods used to identify dispersal (Zeller et al., 2018), even though that was not their primary focus.

Average Euclidean dispersal distance ranged from 9.0 to 483 km (maximum = 24.5-1067 km; Fig. 6) and were typically smaller for females than males (Fig. D7). When compared to the literature data, the mean and the maximum Euclidean dispersal distances for pumas in our study were higher than 55% and 49% of all other studies, respectively (Fig. 6). When compared to males only, the mean and maximum dispersal distances we found were higher than 37.5% and 53% of all studies, respectively (Fig. D8). However, divergent dispersal definitions and methods hinder the possibility of direct comparisons.

Total dispersal distance was reported in only four studies, based on GPS or ARGOS data (Table D6). Mean dispersal age found in the literature was 17.7 months (range = [13.3, 31] months), a value considerably lower than our findings in Southeastern Brazil (Fig. D9). This might have occurred because in our study almost no individual was tracked from their natal range, so the dispersal events we recorded are most probably not natal dispersal events. The fate of individuals was only reported in a minority of studies that presented data at the individual level.

4 Discussion

Our study is the first in Brazil to document and infer puma dispersal behavior using fine-scale GPS data, and one of the first studies of this kind in Latin America. Most tracked individuals dispersed, all males, with one performing a long-distance dispersal of 174 km in straight line and several of them covering a long total dispersal distance – more than 300 km for three of them. Straight line dispersal distances were close to the median distances reported in the literature, what indicates the dispersal distances are representative of the dispersal patterns of pumas elsewhere (Zanin, Palomares, & Brito, 2015; Gonzalez-Borrajo, López-Bao, & Palomares, 2017). However, dispersal ages were higher than those reported in the literature (e.g. Beier, 1995; the only individual with comparable dispersal age was reported by Elbroch et al., 2009 in Patagonia). This might be a result of individuals not being monitored from their natal ranges, but opportunistically from capture sites in temporary home ranges or during transient periods of dispersal. Yet, the discrepancy in dispersal ages between our study and the literature might be related to the necessary translocation of individuals captured in urban areas, to the highly fragmented status of the forest landscapes they inhabit (Fig. 1), or to different movement regimes across their lives (e.g. nomadic behavior, Teitelbaum & Mueller, 2019). None of the females in our study dispersed, making it hard to compare our findings with the philopatry and dispersal patterns from the literature (Oliveira et al., 2021).

We found support to our *fast dispersal* hypothesis: pumas exhibited increased speed and more directional movement during dispersal than during residency, in agreement with previous studies of pumas (Elbroch et al., 2009; Morrison, Boyce, & Nielsen, 2015; Choate, Longshore, & Thompson, 2018) and other large carnivores (Barry et al., 2020). During dispersal, pumas crossed longer daily distances and spent less time around local neighborhoods, using less forest areas and more pasturelands than during residency, even though this pattern varied across individuals. Pumas moved more slowly in forests and Cerrado areas during dispersal, in contrast to pastures that were crossed at higher speeds during dispersal than during ranging behavior, mainly at night. They also moved faster around urban areas during dispersal and within a zone of 1 km around roads during residency at daytime – but not during dispersal and at night. This corroborates our *human disturbance* hypothesis: pumas move more often and faster through areas with more anthropogenic disturbance, mainly at night and during dispersal. In contrast, they spend more time and move more slowly in safe environments such as forest, savannah, and riparian vegetation during in daytime and during residency.

Other studies with pumas also found faster movements in areas with higher proportion of anthropized land use types as agriculture and pasture (Morrison, Boyce, & Nielsen, 2015) and avoidance of croplands and open pastures during residency (Azevedo et al., 2021). Contrary to our expectations, however, we found no difference in movement rates in sugarcane plantations at night between dispersal and residency phases. This might be related to the high use of these areas during residency to hunt prey that stay and use sugarcane plantations, as pumas have been shown to change their diet towards different prey in sugarcane-dominated landscapes (Magioli et al., 2014; Magioli & Ferraz, 2021).

Pumas in Southeastern Brazil had smaller home ranges in landscapes with higher forest amount and lower road density, which supports the *forest importance* hypothesis. Similar to findings for pumas in other areas (Azevedo et al., 2021) and jaguars across their range (J. J. Thompson et al., 2021), our results point to the importance of forests as habitat, with smaller but highly forested areas, with low road density, providing ample prey and shelter (Morato et al., 2016). The *behavioral plasticity* hypothesis, which assumed pumas would not necessarily need larger areas in more anthropized landscapes because of their change in diet (Magioli et al., 2014), was not supported by our data. One explanation may be that a change in pumas feeding patterns towards smaller prey (Magioli & Ferraz, 2021), which is typical in more agriculturally impacted environments, e.g. areas with higher proportion of sugarcane (Magioli et al., 2014), leads to a requirement for larger home ranges than in areas with higher proportions of forest cover and associated larger prey species.

4.1 Conservation and management implications

Our results underscore the vital role of large forest patches in sustaining carnivore populations, echoing several other studies with small and large felids and top-predator species (Morato et al., 2018; Paolino et al., 2018; Azevedo et al., 2021). By showing how pumas move during dispersal in parts of the Atlantic Forest and Cerrado biomes in Southern Brazil, we identify habitat requirements and behaviors during a key life history phase. This knowledge is important in delineating corridors and policies to maintain puma metapopulations in highly fragmented landscapes. Earlier studies found some level of gene flow between populations in the region, but suggested a population bottleneck due to persecution and exacerbated by high numbers of road-killed individuals and direct human-puma conflicts (Miotto et al., 2011, 2012). More recently, genetic analyses found a fine-scale puma population structuring (Saranholi, Chávez-Congrains, & Galetti, 2017), suggesting that even populations of a plastic species can become genetically structured in increasingly human-modified landscapes. Future monitoring projects and studies should focus on using data-driven estimates of landscape suitability and permeability to model connectivity and identify priority areas for conservation and restoration of habitats and connectivity (Van Moorter et al., 2021).

It is difficult to make direct comparison of dispersal parameters across puma populations because of the multiple definitions of dispersal and differences in the way they are operationalized into methods. Beyond the definitions, the identification of dispersal and residency behaviors follows different criteria and is still performed visually in most studies. By using statistical methods that account for ranging and dispersal movement parameters (Barry et al., 2020), we provide a basis for more standardized estimation of transience and ranging phases in animal behavior. In spite of the differences between studies, the Euclidean dispersal distances we found were close to median values from studies in North America, suggesting that in principle these values could be used to parameterize population and connectivity models in Southeastern Brazil (Castilho et al., 2011). However, dispersal ages differed markedly from the literature – with pumas in Brazil dispersing at significantly higher ages than in North America – at least in part because of the lack of population monitoring. This indicates that there are some limitations in using observations from a particular environmental context (e.g. the North American mountain west) to parameterize studies in radically different biomes encompassed by the extensive *Puma concolor* range.

Notwithstanding the increased accessibility and miniaturization of tracking technologies such as GPS collars, studies on movement and dispersal monitoring of pumas continue to be a minority in the Global South (Gonzalez-Borrajo, López-Bao, & Palomares, 2017; LaBarge et al., 2022) – only 1 of the 24 studies we reviewed. Apart from some charismatic species as the jaguars (Morato et al., 2018), the movement behavior of most other carnivores are understudied in Central and South America (Zanin, Palomares, & Brito, 2015; Oliveira et al., 2021). Given that, we call for more studies documenting the movement of these species, including their dispersal. We note, however, that movement ecology studies alone are insufficient and the effective link between individuals and populations requires long-term population studies with pumas and other carnivores. Most puma studies in Latin America focus on the analysis of occurrence and activity patterns using camera trap data (e.g. Lyra-Jorge et al., 2010; Gutiérrez-González & López-González, 2017) and genetic analyses using structured and opportunistic samples (e.g. road kills) of pumas (Miotto et al., 2011; e.g. Gallo et al., 2021). A few studies have been using satellite monitoring on pumas (Elbroch et al., 2009; de la Torre, Núñez, & Medellín, 2017; Azevedo et al., 2021), but these studies are still scarce and generally not linked to population monitoring. This makes it impossible to connect movement behavior to natal dispersal and to infer dispersal causes and their consequences for metapopulation maintenance and connectivity. Given the importance of these species to top-down regulation of ecological communities and their potential role as umbrella and surrogate species in conservation projects, mainly in face of fast-paced forest habitat conversion to urban, agricultural, and pasture areas, we urge that detailed movement studies be conducted in combination with long-term, landscape scale monitoring of populations pumas and other carnivores, to allow the inference of population sizes and how they are affected by dispersal and land use change. Future studies should compare movement patterns among ecoregions, search for thresholds in forest amount and in the composition of landscapes that lead to changes in behavior and occurrence of pumas, and ultimately search for the patterns and mechanisms that explain the behavioral plasticity of this species and the consequences of anthropogenic infrastructure and activity to their populations.

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Declaration of competing interest. The authors declare no competing interests.

Data availability. The GPS data collected and used in this study is stored on MoveBank (Movebank project ID 577226894 – Pumas from Tiete Project; Movebank project ID 594660300 – Onças do Legado) and access to it might be requested to the first author or through contact with Instituto Pró-Carnívoros. Data from the literature compilation and R code for all analyses performed in this study are available in the Github repository: https://github.com/bniebuhr/puma_dispersal_residency_Brazil (private).

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Figures

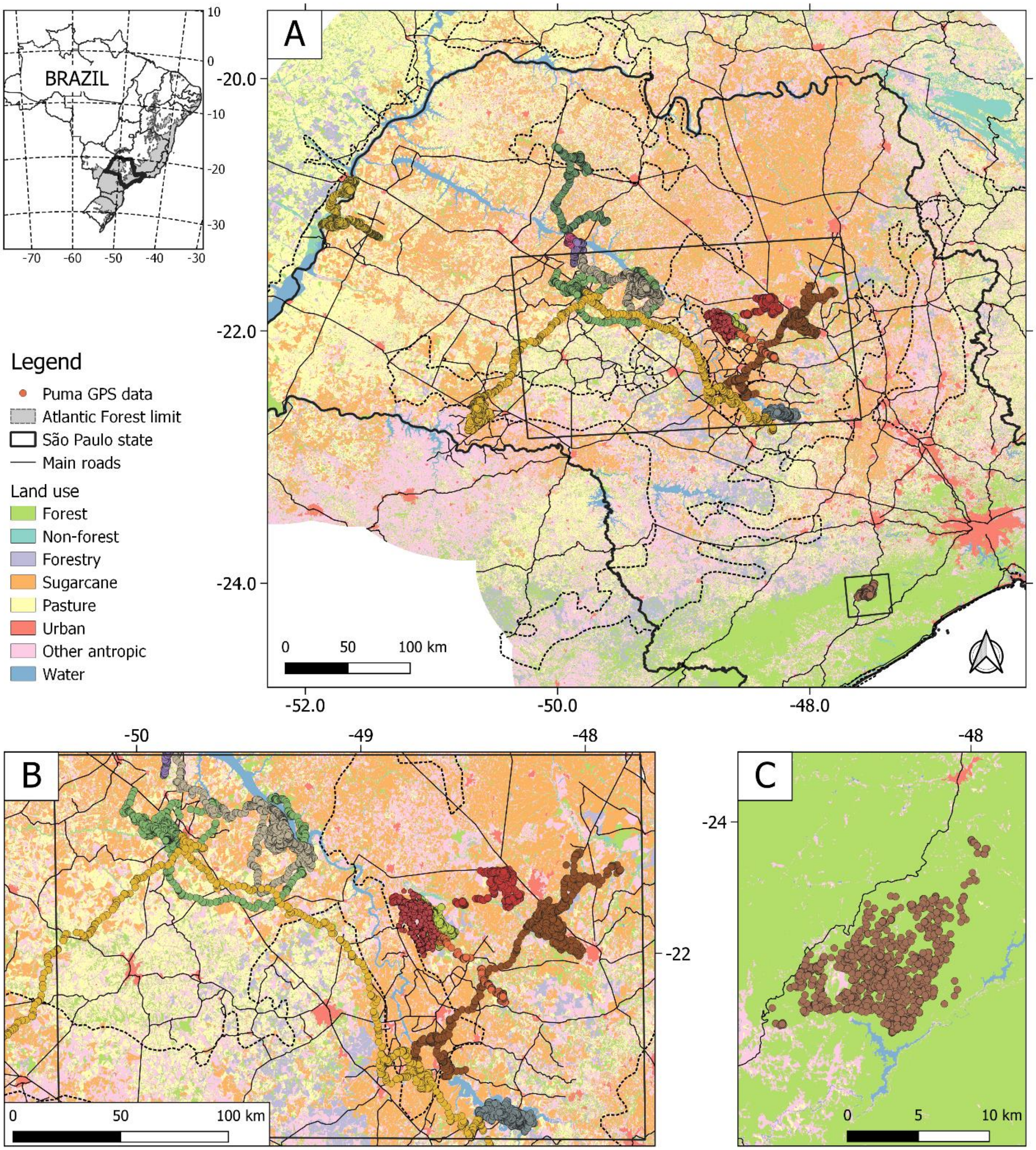

Figure 1. (A) Study area and GPS locations of the puma individuals. (B) Most individuals were monitored along the Tietê river basin in the interior part of São Paulo state, in the transition between small patches of Atlantic Forest and Cerrado. (C) One individual (in the Southeast) was monitored in a continuous forest along the coastal Atlantic Forest. Different point colors represent locations of different individuals. The inset shows the location of the São Paulo state and the Atlantic Forest limit within Brazil.

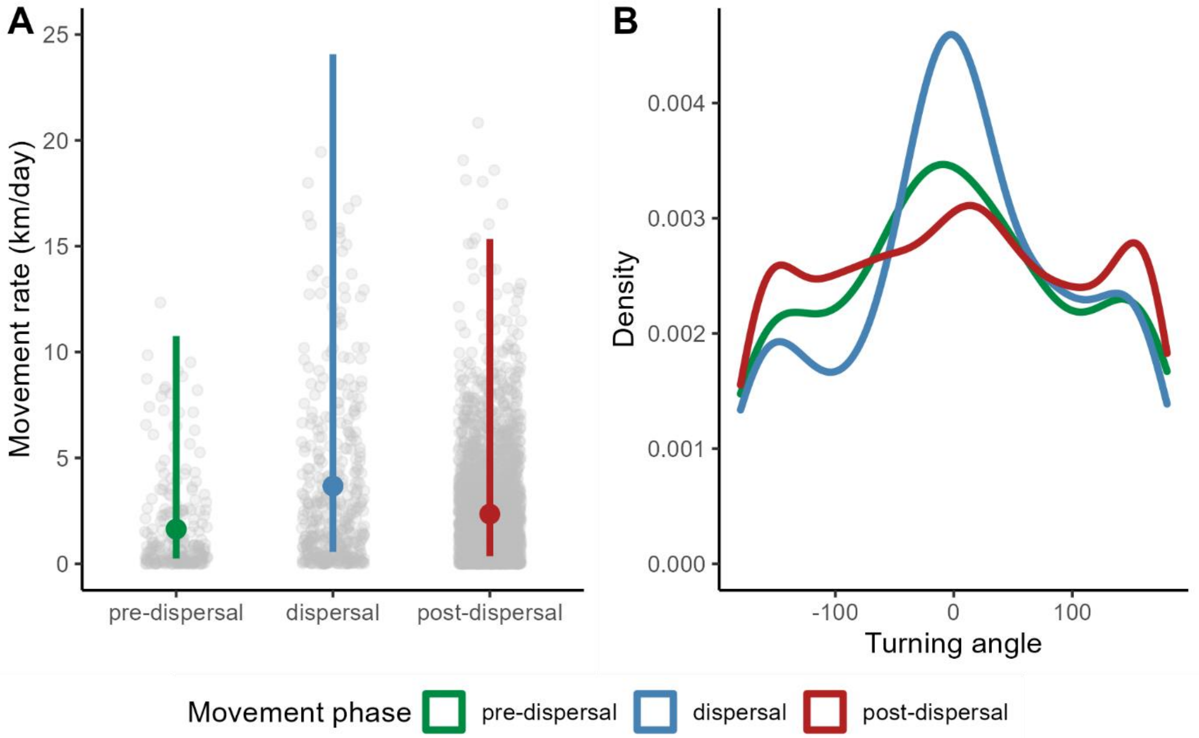

Figure 2. Movement rate and turning angle distributions for the pre-dispersal (n = 7), dispersal (n = 8) and post-dispersal phases (n = 14) of puma movement in Southeastern Brazil. Distances and angles were calculated using one average location per day. Resident animals (n = 6) were considered as in the post-dispersal phase.

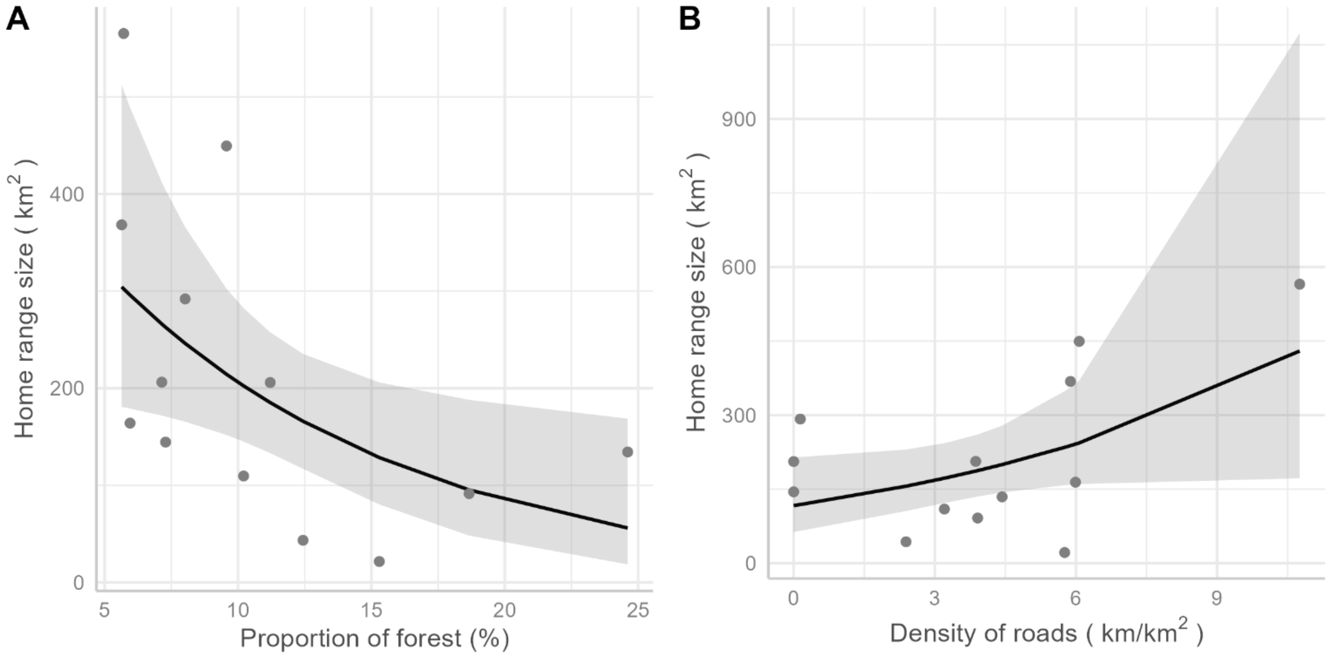

Figure 3. Predicted home range sizes in relation to the proportion of forest and the average density of roads within the home range. Density of roads is represented as the length of roads (in km) per 100km^2.

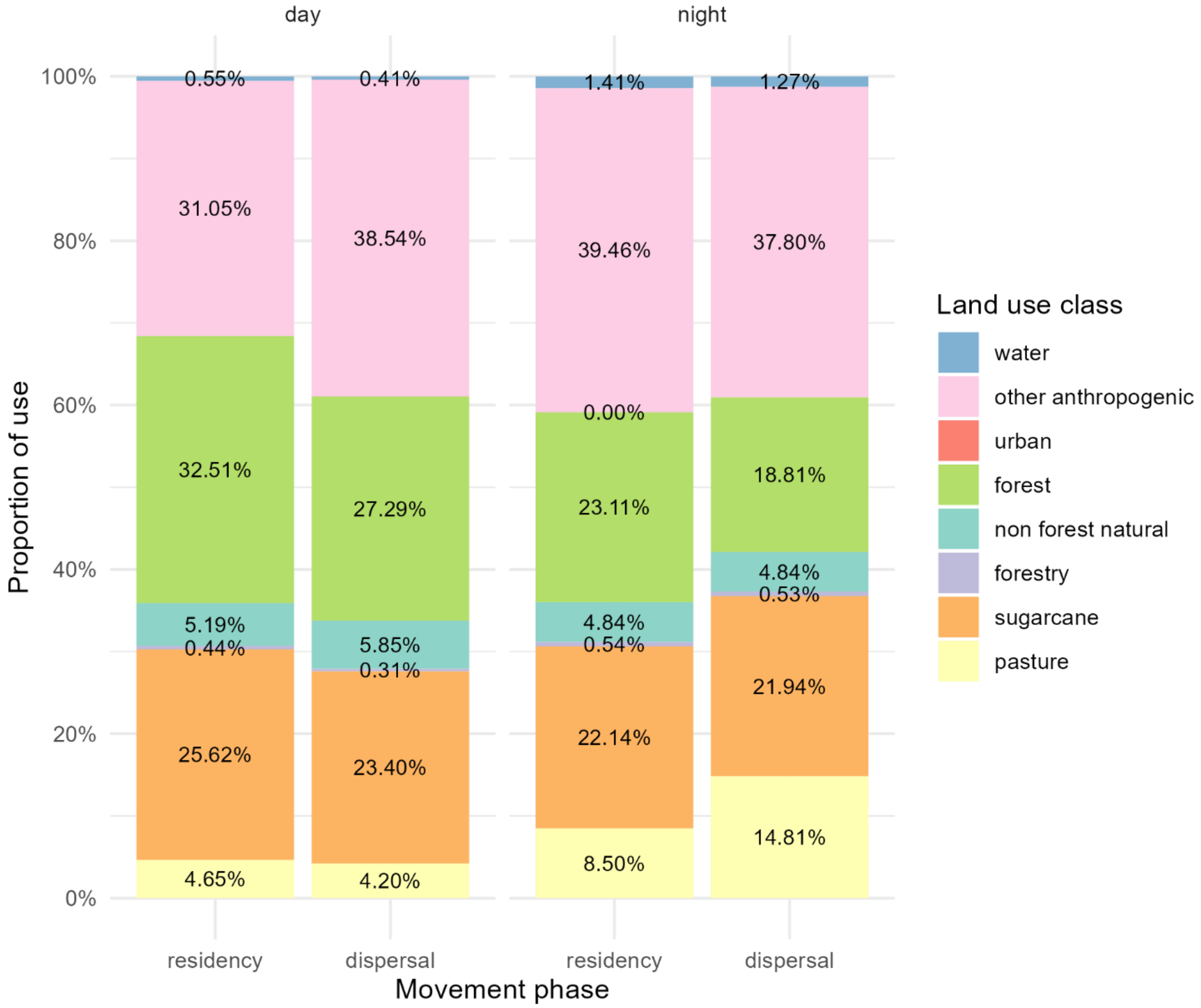

Figure 4. Proportion of puma GPS locations in different land use types, for dispersal and residency phases, during day and night. Other anthropogenic uses consist of agricultural areas (mainly citrus and small areas of coffee or other crops) as well as low productive pastures and bare soil.

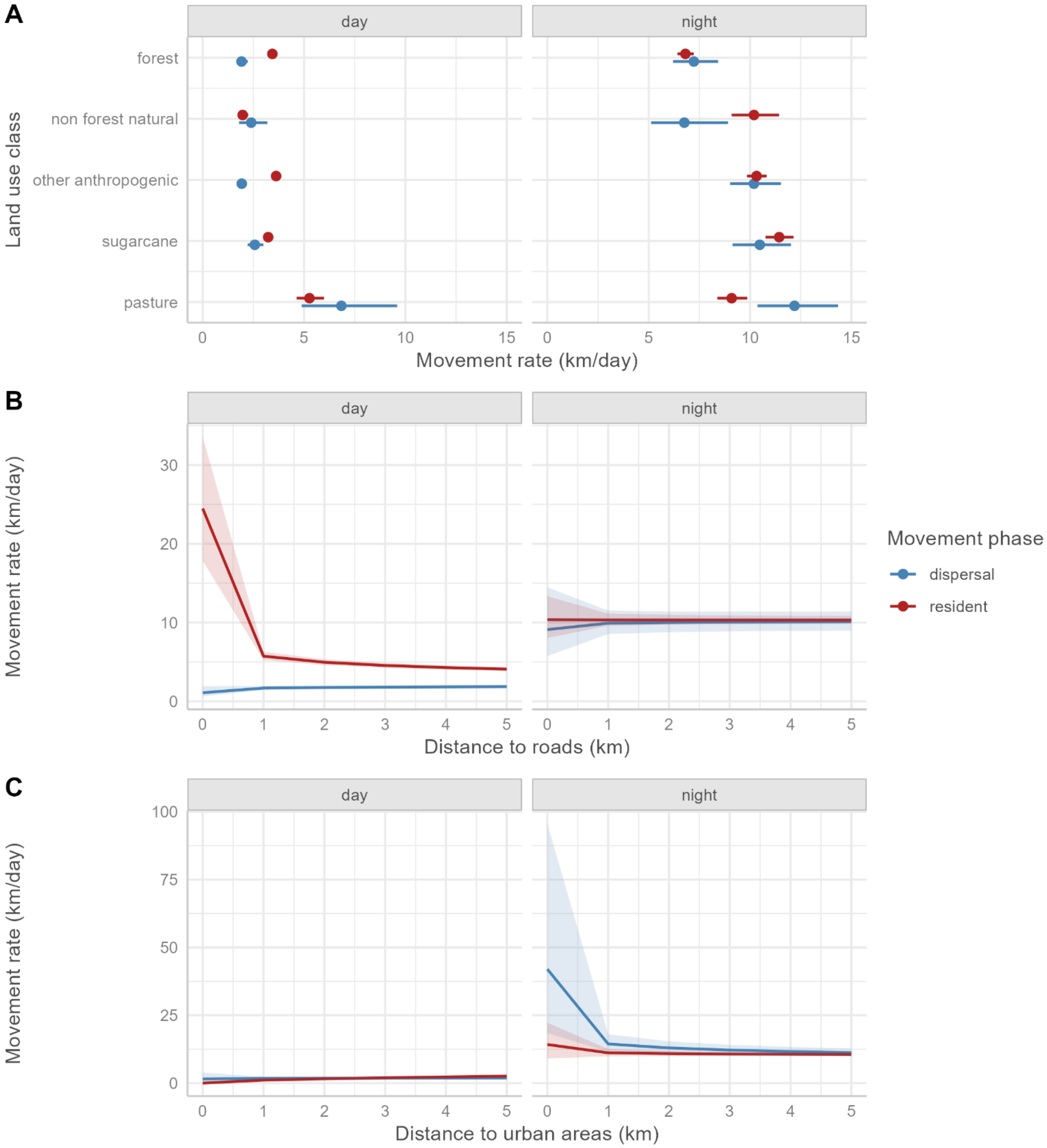

Figure 5. Predicted movement rates of pumas (A) across land use classes and for different distances to (B) roads and (C) urban areas, for dispersal and residency phases, during day and night.

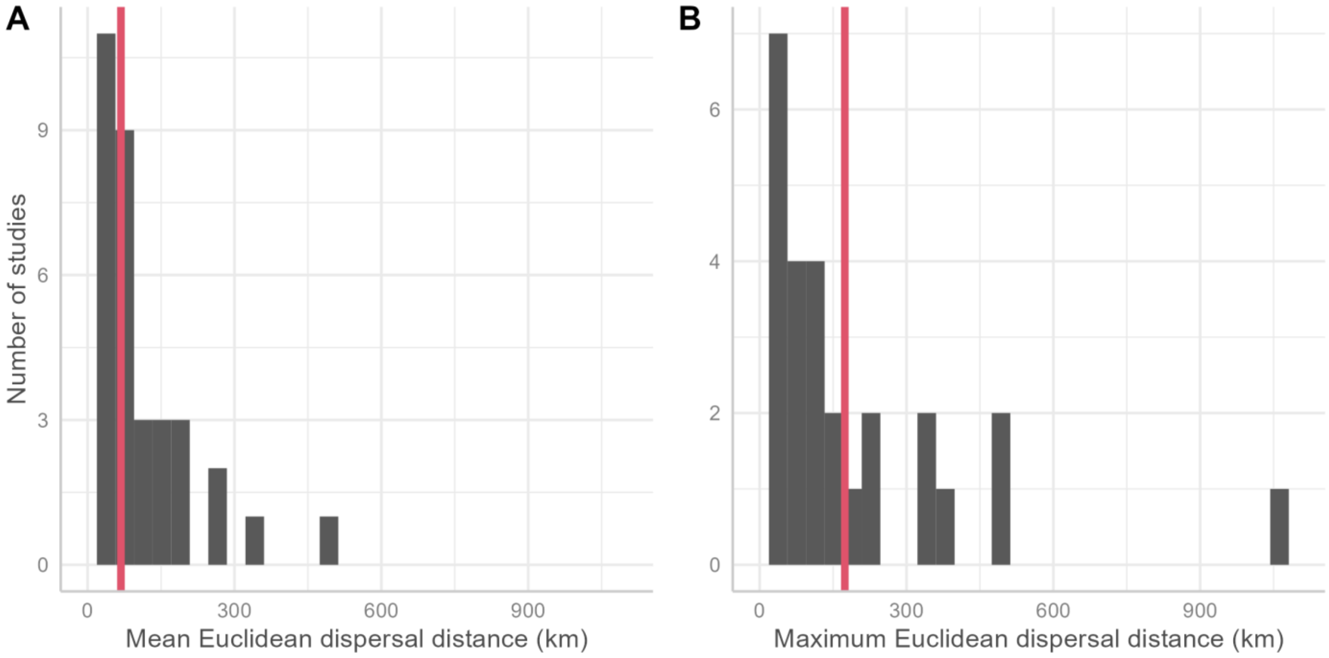

Figure 6. Histogram of (A) mean and (B) maximum Euclidean dispersal distance (i.e., the straight-line distance between the start and end point of the dispersal), including all puma studies listed from the literature (grey bars). The red lines represent mean (in A) and maximum (in B) Euclidean dispersal values estimated in this study for pumas in Southeastern Brazil.

Supplementary Materials

Appendix A

In Appendix A we present additional information on the background maps used in the study. All maps were processed in GRASS GIS environment, version 7.8 (GRASS Development Team, 2020), in Albers Equal Area coordinate system, datum SIRGAS 2000. The Proj4 parameters for the coordinate reference system we used are:

`+proj=aea +lat_1=-2 +lat_2=-22 +lat_0=-12 +lon_0=-54 +x_0=0 +y_0=0 +ellps=GRS80 +units=m +no_defs`

All maps were resampled to resolution of 30 m before analysis.

Table A1. Description of the background maps used for characterizing puma movement patterns. The formal references are found in the main text.

Layer	**Description**	**Year***	**Original resolution (m)**	**Institution**	**Source**
Land cover	Map of land cover and land use manually mapped based on RapidEye satellite images from the year 2013-2014. The map presents 6 classes: forest, non-forest natural vegetation, water, urban, forestry, and anthropic use. Vector.	2013	5	Fundacão Brasileira para o Desenvolvimento Sustentável (FBDS)	[1]
Sugarcane	Map of sugarcane plantations, based on images from Landsat, CBERS e Resourcesat-I. Vector.	2013-2014	30	Instituto Nacional de Pesquisas Espaciais (INPE)	[2]
Pasture	Map of pastures from Brazil, based on Landsat satellite images. Raster.	2015	30	Laboratório de Processamento de Imagens e Geoprocessamento (LAPIG), Universidade Federal de Goiás	[3]
Roads	Map of main roads of Brazil. Vector. The map was manually edited to add large state or municipal roads from the State of São Paulo.	2013	30	Departamento Nacional de Infraestrutura de Transportes (DNIT)	[4]
Road density	Map of road density, based on the map of roads, measured as km of roads per 100 km^2. The map was calculated in GRASS GIS using the *r.neighbors* (size = 333 pixels or 10km) and *r.mapcalc* tools.	2013	30	Derived variable	This study

Distance to roads	Map of distance from each pixel to the nearest road. The map was computed in GRASS GIS using the *r.grow.distance* tool.	2013	30	Derived variable	This study
Urban density	Map of urban density, based on the land cover class of urban areas, measured as number of 30x30 m^2 pixels of urban areas per 100 km^2. The map was calculated in GRASS GIS using the *r.neighbors* (size = 333 pixels or 10km) and *r.mapcalc* tools.	2013	30	Derived variable	This study
Distance to roads	Map of distance from each pixel to the nearest urban area. The map was computed in GRASS GIS using the *r.grow.distance* tool.	2013	30	Derived variable	This study
Distance to water bodies	Map of distance from each pixel to the nearest water body, using the land cover class of water as input. The map was computed in GRASS GIS using the *r.grow.distance* tool.	2013	30	Derived variable	This study

*For the derived variables, the year represents the corresponding year of the original data.

1. http://geo.fbds.org.br/. Reference: FBDS (2017).
2. http://www.dsr.inpe.br/laf/canasat/. Reference: Rudorff et al. (2010).
3. https://pastagem.org/atlas. Reference: Parente et al. (2017).
4. http://servicos.dnit.gov.br/vgeo/; http://www.metadados.inde.gov.br/geonetwork/srv/br/metadata.show?id=46093&currTab=simple. Reference: DNIT (2013).

Appendix B

In Appendix B we present details on the methods used to analyze the puma movement data.

Detailed study area description

The study was conducted in the ecotone between two biodiversity hotspots, Atlantic Forest and Cerrado, in the state of São Paulo, Brazil. The Atlantic Forest is a highly biodiverse biome and one of the most fragmented in Brazil, with only about 23% of remaining forests (Vancine et al., 2023). The Brazilian Cerrado is the largest Savannah in the Americas and the richest in species worldwide. It harbors about 30% of the Brazilian biodiversity, yet only about 50% of the native vegetation remains (Project MapBiomas, 2020). In São Paulo, the Atlantic Forest is composed of a few large patches of subtropical moist rainforest close to the coast and many small deciduous and semi-deciduous forest patches in the countryside (Vancine et al., 2023). The Cerrado in São Paulo is composed of a combination of semi-deciduous forests and savannahs. The study area is seasonally marked by a tropical climate, with dry winters, from May to October, and rainy summers, from November to April. The average temperature of the coldest month is above 18ºC. Annual precipitation is above 750 mm, reaching up to 1800 mm (CEPAGRI-UNICAMP, 2020).

Most pumas were captured and monitored along the Tietê River basin, in a region encompassing the cities of Promissão, Ibitinga and Barra Bonita (21°46'04" S, 48°59'07" W; Fig. 1 of the main text). The area is dominated by anthropogenic land use types, mainly sugarcane plantations (63,000 km^2, 25.4% of the state), pasture lands for cattle production (52,300 km^2, 21%) and other anthropic uses (mainly forestry, which covers 10,200 km^2 or 4.1% of the state, and citrus, soybean, and coffee plantations, which together with other crops cover 15,500 km^2, 6.2%; Project MapBiomas, 2020). Forests represent only 52,000 km^2 (20% of the land), even though the major part is located in a few continuous forest patches by the coast, far from where these individuals were monitored. In the Tietê river watershed, only 13% of the area corresponds to forest (Project MapBiomas, 2020; Fig. 1 of the main text). The largest Brazilian urban areas and industrial complexes are located in the state of São Paulo. Even though urban areas cover only 3% (7,700 km^2) of the state, they are inhabited by about 44 million people. The state is traversed by dozens of large and small roads, which are daily used by millions of people to move between cities and by trucks to transport crops towards the largest port of the country, in Santos.

GPS monitoring and data handling

GPS data wrangling was done in R with packages *dplyr* (Wickham et al., 2021), *tidyr* (Wickham, 2021), and *purrr* (Henry & Wickham, 2020). Step lengths, turning angles, and other movement parameters were computed with the package *amt* (Signer, Fieberg, & Avgar, 2019). Since collars were programmed to record one position per hour, locations that were recorded more than 1.5 h apart from each other were separated in different movement bursts, so that no displacement was considered for these intervals. This made the total number of positions analyzed slightly smaller than the total number of animal positions recorded.

Identifying and characterizing residency and dispersal

To identify the timing of departure from residency, dispersal, and settling, we adapted code from Barry et al. (2020) and implemented functions in the R package *disperser* (Gurarie et al., under development). As described in the main text, the residency behavior is represented by an Ornstein-Uhlenbeck-Fleming (OUF) model (Fleming & Calabrese, 2017) and approximated by a ARMA(1,1) model. Likewise, dispersal is represented by a continuous velocity model (CVM) and approximated by an ARIMA(1,1,0) model. The R functions we built set likelihood functions to the change in (x,y) positions and optimize them to find the most likely departure and settling dates using either of five candidate models: (i) residency only (movement characterized by an OUF model, no transition between behaviors); (ii) dispersal only (movement characterized by a CVM model, no transition between behaviors) (iii) departure (OUF model and transition to a CVM model); (iv) settling (CVM model followed by a transition to an OUF model), and (v) depart-settle (two OUF models separated by a phase with movement characterized by a CVM model). For each individual, all five models were fitted and compared through Akaike Information Criterion (AIC). The model with lowest AIC was considered the most plausible to explain the behavior and timing of transition between behaviors (Burnham, Anderson, & Huyvaert, 2011).

Once the timing of transitions and the behaviors were identified, the movement patterns during each movement phase (pre-dispersal, dispersal, post-dispersal) were characterized by fitting generalized linear mixed models to the movement rates (distance traveled by day) and turning angles (angles between average subsequent daily positions) considering the model structure `y ~ movement_phase + (1|id)`, where `id` is the individual ID and `y` followed a Gamma distribution with logarithmic link for the movement rate and a von Mises distribution for the turning angles. All the analyses for identifying and characterizing residency and dispersal were based on a rarefied dataset with only one average position per day, to guarantee regularity. Movement parameters were computed with the *amt* package (Signer, Fieberg, & Avgar, 2019) and analyzed using the *glmer* function from the *lme4* package in R (Bates et al., 2015, p. 4) and the *circular* package for turning angles (Agostinelli & Lund, 2022). Predictions from the models were made with the function *ggpredict* from the *ggeffects* package (Lüdecke, 2018).

Home range analysis

Home ranges were calculated by computing variograms and estimating continuous-time movement models using the *ctmm* package (Calabrese, Fleming, & Gurarie, 2016), as explained in the main text. Variograms were built using the *variogram* function and used to qualitatively assess which individuals and movement phases had a stationary variogram, representing a home range behavior (Fleming et al., 2014). In this process, all the (generally short) pre-dispersal residency phases were removed from the analyses, and only the post-dispersal residency phases were analyzed. Initial parameters for fitting the continuous time movement models were computed with the *ctmm.guess* function and the models were fit through the *ctmm.fit* function. To ease the computation of home ranges using multiple estimators and the comparison with literature data (mostly based on minimum convex polygons, MCP, and traditional kernel density estimation, KDE), we fitted the *ctmms* using the functions *hr_mcp*, *hr_kde*, and *hr_akde_auto* from the *amt* package (Signer & Fieberg, 2021). Home range sizes were computed taking the estimates from the 95% AKDE isopleth polygons, through the function *st_area* from the *sf* package (Pebesma, 2018). As mentioned in the main text, even though no formal analysis was made to account for the reservoirs as barriers in the residency behavior, the parts of the polygons within the reservoirs were removed using the *st_difference* function from the *sf* package (Pebesma, 2018), using polygons mapping these reservoirs areas.

To relate home range sizes to the landscape, we extracted the land use environmental information for the 95% AKDE polygons and computed the proportion of the polygon that was covered by the main land use classes (forest, non-forest natural areas, forestry, sugarcane, pasture) as well as average values of urban density, road density, and distance to urban areas, roads, and water bodies. The data was extracted in the polygon delimitation using the function *extract* from the *terra* package (Hijmans, 2022). All covariates were scaled to mean 0 and standard deviation 1 prior to model fitting. The relationship between home range sizes and landscape variables was accessed through generalized linear models using Gamma response and a logarithmic link, through the *glm* function from the *stats* package in R (R Core Team, 2020). Since the land use classes are generally correlated, we fitted models including each of them at a time, besides the mean density of roads and mean distance to urban areas. Mean distance to water was non-significant in all models and was removed from the fitted models. Models were compared through AIC corrected for small samples (AICc) using the *bbmle* package (Bolker & R Development Core Team, 2021) and the ones with lowest AICc were selected. Predictions were made with the *ggpredict* function from the *ggeffects* package (Lüdecke, 2018). One individual (Jussara) who inhabited the coastal Atlantic Forest was removed from this analysis, since it was a clear outlier in terms of proportion of forest within the home range. In the end, we used n = 13 individuals for the analysis. We could not include sex in the models because of the low number of females (n = 2). Correlation was evaluated between all pairs of covariates, and covariates with correlation coefficient higher than 0.6 were not included in the same model.

Effects of the landscape on ranging and dispersal

To evaluate habitat use by pumas, we annotated the 1h-fix rate positions with the environmental data using the R package *raster* at the starting point of each movement step and computed the proportion of positions in each land use type for each movement phase (residency and dispersal; both pre- and post-dispersal phases were considered as residency) and time of the day (day, night). The distinction between times of the day for each position was made using the function *time_of_day* from the package *amt* (Signer, Fieberg, & Avgar, 2019), which is a wrapper to other functions from the *maptools* package (Bivand & Lewin-Koh, 2021).

The effects of landscape and infrastructure variables on puma movement rates were assessed through generalized linear models with Gamma response and logarithmic link using the step lengths (rescaled to km/day, and called here as movement rates) as a response variable and adding individual sex, movement phase, time of the day, land use class, and distance to roads, urban areas and water bodies as fixed effects. The interactions between movement phase and time of the day were also included for land use and the distances to roads, urban areas, and water bodies. A full model was fitted and compared to subsets of models where some of these variables were removed. Models were compared through AIC and the model with lowest AIC was considered the most parsimonious. We also fitted and compared alternative models including the density of roads and urban areas as covariates instead of distance to the nearest features. However, the models with distance variables performed better (lower AIC). Models for landscape effects on movement were fitted considering 1h-fix rate movement data. Correlation was evaluated between all pairs of covariates, and covariates with correlation coefficient higher than 0.6 were not included in the same model. Models were fit with the *glm* function from the *stats* package (R Core Team, 2020). Mean step lengths were predicted by multiplying the shape and scale parameters of the fitted Gamma distribution using the function *ggpredict* from the *ggeffects* package (Lüdecke, 2018).

Literature compilation

We compiled studies in a non-comprehensive search with the aim of putting the dispersal patterns found for pumas in Southeastern Brazil into context within the state-of-the-art on the dispersal ecology of the species. The search procedure is described in the main text. We kept only studies that had within their aims the estimation of dispersal events, transitions between residency and dispersal, dispersal ages, or dispersal distances, and possibly other aspects of puma spatial ecology, like home ranges, habitat selection, population or metapopulation dynamics. Studies that used data on dispersers to perform other analyses (e.g. Zeller et al., 2018) were reviewed but not included in the final list of studies. When available, we recorded, from each study: dispersal age, fate after dispersal, monitoring method (e.g. VHF, GPS), method to estimate the dispersal phase, and dispersal distance (Euclidean and total dispersal distance), both for each individual (when reported) or averages, standard deviations, and minimum/maximum values for the set of monitored individuals. After the compilation, we plotted histograms and forest plots of Euclidean dispersal distances and ages for the published studies and compared them with the values found in our study. We did the same for total dispersal distances. The complete list of studies selected is found in Appendix C.

Appendix C

In the Appendix C we present the list of papers included in the review of puma dispersal studies.

Below as present the list of studies which included estimating dispersal phase, distance, age, or other dispersal parameters as one of the main aims. These studies were used to compare dispersal distances and ages with the parameters found in our study for pumas in Southeastern Brazil.

1. Anderson, A., Bowden, D. C., & Kattner, D. M. (1992). The puma on the Uncompahgre Plateau, Colorado. Colorado Division of Wildlife Technical Publication 40, Denver, CO. 116 pp.
   Not accessed directly; dispersal parameters were reported by Stoner et al. (2008) and Choate et al. (2018).

2. Ashman, D., Christensen, G. C., Hess, M. L., Tsukamoto, G. K., & Wickersham, M. S. (1983). The mountain lion in Nevada. (Final Report P-R Proj.W-48-15). p. 75. Nevada Fish and Game Department.
   Not accessed directly; dispersal parameters were reported by Choate et al. (2018).

3. Beier, P. (1995). Dispersal of Juvenile Cougars in Fragmented Habitat. *The Journal of Wildlife Management* 59, 228.

4. Choate, D. M., Longshore, K. M., & Thompson, D. B. (2018). Cougar Dispersal and Natal Homing in a Desert Environment. *Western North American Naturalist* 78, 221–235.

5. Elbroch, M., Wittmer, H. U., Saucedo, C., & Corti, P. (2009). Long-distance dispersal of a male puma (*Puma concolor puma*) in Patagonia. *Rev. Chil. Hist. Nat.* 82.

6. Hawley, J. E., Rego, P. W., Wydeven, A. P., Schwartz, M. K., Viner, T. C., Kays, R., Pilgrim, K. L., & Jenks, J. A. (2016). Long-distance dispersal of a subadult male cougar from South Dakota to Connecticut documented with DNA evidence. *J. Mammal.* 97, 1435–1440.

7. Hemker, T. P., Lindzey, F. G., & Ackerman, B. B. (1984). Population Characteristics and Movement Patterns of Cougars in Southern Utah. *The Journal of Wildlife Management* 48, 1275.

8. Hornocker, M. G. (1970). An Analysis of Mountain Lion Predation upon Mule Deer and Elk in the Idaho Primitive Area. *Wildlife Monographs* 3–39.

9. Lindzey, F. G., Sickle, W. D. V., Ackerman, B. B., Barnhurst, D., Hemker, T. P., & Laing, S. P. (1994). Cougar Population Dynamics in Southern Utah. *The Journal of Wildlife Management* 58, 619.

10. Logan, K. A., Irwin, L. L., & Skinner, R. (1986). Characteristics of a Hunted Mountain Lion Population in Wyoming. *The Journal of Wildlife Management* 50, 648.

11. Logan, K. A., & Sweanor, L. L. 2000. Puma. Pages 347–377 in S. Demarais and P. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

12. López-González, C. A. (1999). Implicaciones para la conservación y el manejo de pumas (*Puma concolor*) utilizando como modelo una población suejta a caceria deportiva (PhD Dissertation). Universidad Nacional Autonoma de Mexico, Mexico.

13. Maehr, D. S., Land, E. D., & Roof, J. C. 1991. Social ecology of Florida panthers. *Natl. Geogr. Res. and Explor.* 7, 414-431.
    Not accessed directly; dispersal parameters were reported by Beier (1995).

14. Maehr, D. S., Land, E. D., Shindle, D. B., Bass, O. L., & Hoctor, T. S. (2002). Florida panther dispersal and conservation. *Biological Conservation* 106, 187–197.

15. Morrison, C. D., Boyce, M. S., & Nielsen, S. E. (2015). Space-use, movement and dispersal of sub-adult cougars in a geographically isolated population. *PeerJ* 3, e1118.

16. Newby, J. R., Scott Mills, L., Ruth, T. K., Pletscher, D. H., Mitchell, M. S., Quigley, H. B., Murphy, K. M., & DeSimone, R. (2013). Human-caused mortality influences spatial population dynamics: Pumas in landscapes with varying mortality risks. *Biological Conservation* 159, 230–239.

17. Ross, P. I., & Jalkotzy, M. G. (1992). Characteristics of a Hunted Population of Cougars in Southwestern Alberta. *The Journal of Wildlife Management* 56, 417.

18. Spreadbury, B. R., Musil, R. R. K., Musil, J., Kaisner, C., & Kovak, J. (1996). Cougar Population Characteristics in Southeastern British Columbia. *The Journal of Wildlife Management* 60, 962.

19. Stoner, D. C., Rieth, W. R., Wolfe, M. L., Mecham, M. B., & Neville, A. (2008). Long-Distance Dispersal of a Female Cougar in a Basin and Range Landscape. *Journal of Wildlife Management* 72, 933–939.

20. Stoner, D. C., Wolfe, M. L., Mecham, C., Mecham, M. B., Durham, S. L., & Choate, D. M. (2013). Dispersal behaviour of a polygynous carnivore: do cougars Puma concolor follow source-sink predictions? *Wildlife Biology* 19, 289–301.

21. Sweanor, L. L., Logan, K. A., & Hornocker, M. G. (2000). Cougar Dispersal Patterns, Metapopulation Dynamics, and Conservation. *Conservation Biology* 14, 798–808.

22. Thompson, D. J., & Jenks, J. A. (2010). Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization. *Ecosphere* 1, art8.

23. Thompson, Daniel J., & Jenks, J. A. (2005). Long-distance dispersal by a subadult male cougar from the Black Hills, South Dakota. *Journal of Wildlife Management* 69, 818–820.

24. Weaver, J. L., Paquet, P. C., & Ruggiero, L. F. (1996). Resilience and Conservation of Large Carnivores in the Rocky Mountains. *Conservation Biology* 10, 964–976.

Below we show a list of other studies that were used as a reference for the contextualization of puma dispersal and spatial ecology, even though they were not compared directly. These include studies that performed dispersal analysis but did not have the dispersal parameter estimation as a focus, studies with subsamples of individuals that were included in other studies in the list above, as well as reviews and compilation studies.

1. Gonzalez-Borrajo, N., López-Bao, J. V., & Palomares, F. (2017). Spatial ecology of jaguars, pumas, and ocelots: a review of the state of knowledge. *Mam Rev* 47, 62–75.

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5. Zanin, M., Palomares, F., & Brito, D. (2015). What we (don't) know about the effects of habitat loss and fragmentation on felids. *Oryx* 49, 96–106.

6. Zeller, K. A., Jennings, M. K., Vickers, T. W., Ernest, H. B., Cushman, S. A., & Boyce, W. M. (2018). Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Divers Distrib* 24, 868–879.

7. Zeller, K. A., Vickers, T. W., Ernest, H. B., & Boyce, W. M. (2017). Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. *PLoS ONE* 12, e0179570.

Appendix D

In the Appendix D we present additional analysis, figures, and tables to understand the dispersal behavior of pumas in Southeaster Brazil.

Table D1. Characteristics of the puma individuals monitored: sex, weight and age when collared and released, years when it was monitored, sample size (n) and number of days monitored, behavior (resident or disperser), whether it was translocated (and the reason), and fate.

Name	**Sex**	**Weight (kg)**	**Age (months)**	**Years**	**Days monitored**	**n**	**Behavior**	**Translocated**	**Fate**
Jussara	F	26	36	2017-2018	166	2577	resident	No	Collar stopped working, individual status unknown
Porã	F	39	48	2016	131	2544	resident	No	Collar stopped working, individual alive, checked with VHF monitoring
Sucuri	F	42	48	2015	93	1994	resident	No	Predated by a Sucuri snake
Araçatuba	M	54	22	2015-2016	315	6159	dispersed	Yes. After 8 months in captivity because of health issues, it was released 100 km from the capture site.	Died from unknown reasons
Kurupi	M	45	42	2019	97	2172	dispersed	Yes	Died from natural causes
Marco	M	42	36	2019-2020	243	4322	resident	No	Collar stopped working, individual alive
Mineiro	M	32	36	2018-2019	348	7252	dispersed	Yes. Captured within an urban area, it was released 30 km	Died from septicemia

								from the capture site.	
Nick	M	46	30	2015-2016	408	8044	dispersed	No	Collar was dropped off, individual alive
Pepira	M	31	24	2019-2020	245	2648	dispersed	No	Collar stopped working, individual alive, checked with camera traps
Piloto	M	41	36	2018-2019	346	6037	dispersed	Yes. Captured within an urban area, it was released 20 km from the capture site.	Poached by hunters in Paraná State
Rafiki	M	31	18	2019-2020	339	7189	resident	No	Collar stopped working, individual alive
Tupã	M	40	42	2019	95	1642	dispersed	No	Died from natural causes after a fight with wild boars
Zeus	M	60	66	2018-2019	146	2436	resident	No	Collar stopped working, individual alive as checked with camera traps
Zorro	M	39	24	2020	105	2061	dispersed	Yes. Captured within an urban area, it was released 40 km from the capture site.	Collar stopped working, individual status unknown

Table D2. Dispersal characteristics for each dispersing puma. The columns present the age of the individual when dispersal started, dispersal start and end dates, dispersal duration, Euclidean dispersal distance, total dispersal distance, and whether the individuals dispersed right after they were collared and released.

Name	Captured as disperser	Dispersal age	Dispersal start	Dispersal end	Dispersal duration (days)	Euclidean dispersal distance (km)	Total dispersal distance (km)
Araçatuba	Yes	22	2015-09-18	2016-02-05	140	54.2	470.4
Kurupi	No, but dispersed on day 6	42.2	2019-08-06	2019-09-17	36	54.8	233.2
Mineiro	No, dispersed on day 50	37.7	2018-08-07	2018-08-25	17	76.9	178.4
Nick	No, but dispersed on day 14	30.5	2015-07-27	2015-10-26	90	67.9	524.9
Pepira	No, but dispersed on day 11	24.7	2019-07-20	2019-08-14	24*	18.7*	28.3*
Piloto	No, dispersed on day 86	38.9	2019-03-08	2019-04-04	26	174	310.8
Tupã	No, dispersed in day 55	43.8	2019-09-01	2019-09-26	24	44.5	50.6
Zorro	No, but dispersed on day 8	24.3	2020-04-23	2020-06-19	56	53.3	249.5

*For this individual, there were gaps in the GPS data, so the estimates for dispersal duration and distance are underestimated and unreliable.

Table D3. Home range estimates for the 14 pumas monitored in this study, using different estimators: minimum convex polygon (MCP), traditional kernel density estimation (KDE), and autocorrelated kernel density estimation (AKDE). MCP and KDE were computed mainly to be able to compare the home range sizes with values from the literature.

Name	Sex	MCP	KDE	AKDE
Jussara	F	71.97	86.21	116.54
Pora	F	64.3	69.33	109.66
Sucuri	F	61.39	69.6	91.5
Aracatuba	M	37.16	40.24	43.45
Kurupi	M	158.09	250.29	565.21
Marco	M	111.52	130.26	134.38
Mineiro	M	209.75	158.79	206.25
Nick	M	135.75	114	144.53
Pepira	M	152.38	125.6	164.07
Piloto	M	270.91	256.46	368.26
Rafiki	M	191.48	120.73	205.91
Tupa	M	5.69	12.39	21.62
Zeus	M	247.05	271.47	291.97
Zorro	M	83.09	134.68	449.44

Table D4. Table of comparison between the models fitted to explain home range size, with data from n = 13 pumas. AICc = Akaike information criterion corrected for small samples. ΔAICc = difference in AICc between the most likely model (shown on top) and each of the other models. df = degrees of freedom. wAICc = AICc weights. The land use classes (forest, non-forest natural areas, forestry, sugarcane) were computed as proportions, road as the average road density, and urban as the average distance to urban areas.

Model	AICc	ΔAICc	df	wAICs
home_range_area ~ forest + road + urban	175.37	0	5	0.522
home_range_area ~ non-forest + road + urban	177.09	1.72	5	0.221
home_range_area ~ forestry + road + urban	177.47	2.10	5	0.183
home_range_area ~ sugarcane + road + urban	179.29	3.92	5	0.074

Table D5. Coefficients of the models fitted to explain home range size, with data from n = 13 pumas. Term = term related to each covariate. Estimate = estimate of the coefficient. SE = standard error of the estimate of the coefficient. t-statistic = t-statistic describing the test for significance for each term. p = p-value (values < 0.05 are marked in bold).

Model	Term	Estimate	SE	t-statistic	p
home_range_area ~ forest + road + urban	**(Intercept)**	**5.24**	**0.16**	**31.27**	**<0.001**
	scale(forest)	**-0.50**	**0.22**	**-2.27**	**0.049**
	scale(road)	0.36	0.19	1.86	0.095
	scale(urban)	0.30	0.24	1.22	0.25
home_range_area ~ non-forest + road + urban	**(Intercept)**	**5.27**	**0.18**	**27.99**	**<0.001**
	scale(non-forest)	-0.46	0.22	-2.06	0.068
	scale(road)	0.07	0.23	0.33	0.749
	scale(urban)	-0.19	0.23	-0.81	0.436
home_range_area ~ forestry + road + urban	**(Intercept)**	**5.28**	**0.18**	**28.06**	**<0.001**
	scale(forestry)	0.31	0.20	1.54	0.156
	scale(road)	0.18	0.21	0.86	0.408
	scale(urban)	-0.10	0.22	-0.46	0.651
home_range_area ~ sugarcane + road + urban	**(Intercept)**	**5.31**	**0.20**	**25.72**	**<0.001**
	scale(prop)	0.21	0.23	0.92	0.38
	scale(road)	0.19	0.24	0.80	0.444
	scale(urban)	0.01	0.24	0.04	0.966

Table D6. Studies that measured total dispersal distance for one or more individuals. When n > 1, mean, minimum and maximum values for the total dispersal distance were recorded.

Study	**Country**	**Year**	**Sex**	**n**	**Mean Euclidean dispersal distance (km)**	**Mean total dispersal distance (km)**	**Minimum total dispersal distance (km)**	**Maximum total dispersal distance (km)**
Stoner et al. 2008	US	2008	F	1	357	1341	NA	NA
Morrison et al 2015	Canada	2015	F	3	13.7	132.1	54.6	209.6
Elbroch et al 2009	Chile	2009	M	1	167	757.4	NA	NA
Morrison et al 2015	Canada	2015	M	4	165.3	364.3	200.9	749.3
Choate et al 2018	US	2018	M	1	33.7	283.89	NA	NA
Our study	Brazil	2023	M	8	68.04	288.3	50.6	524.9

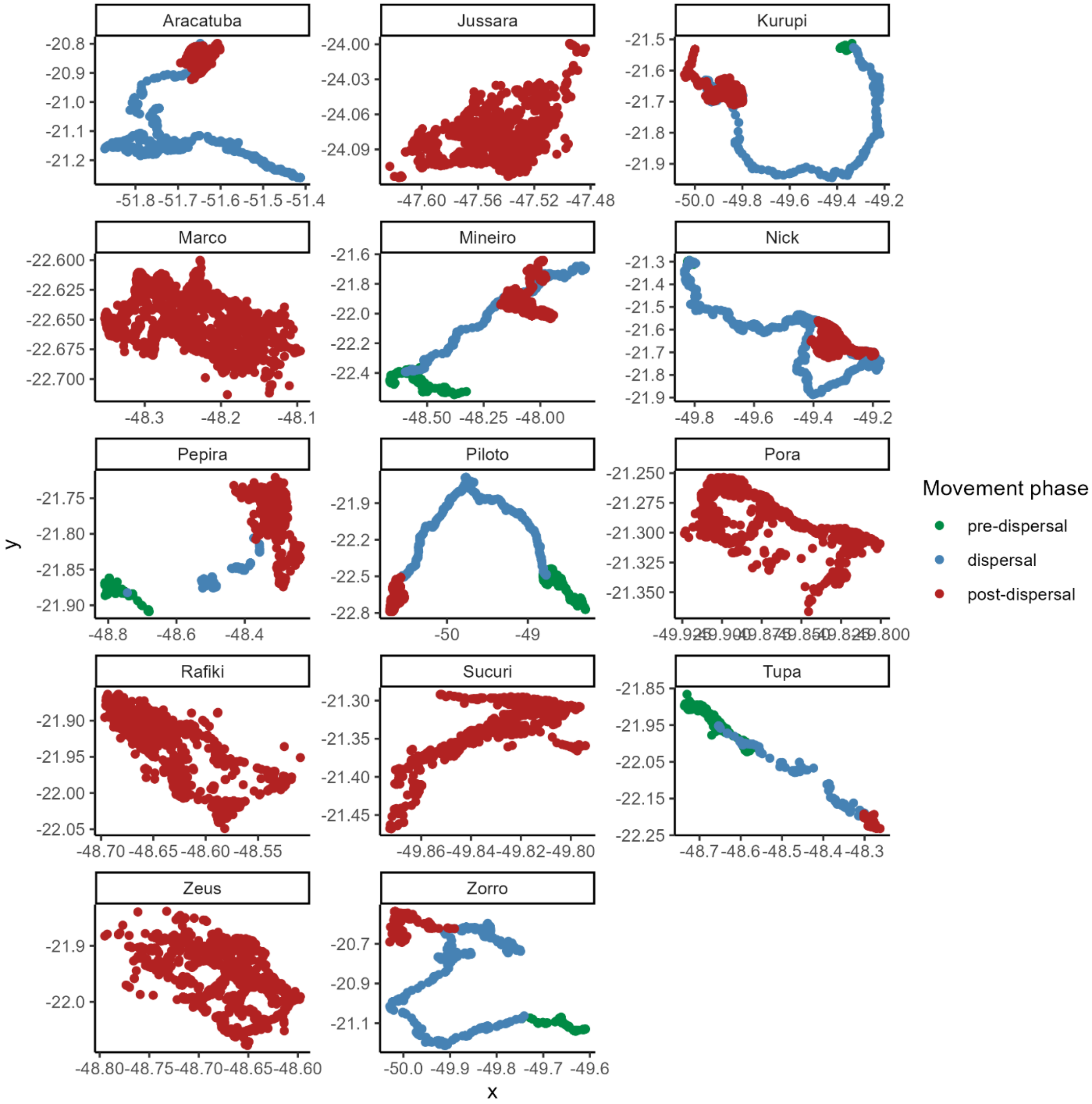

Figure D1. Positions of monitored pumas in each movement phase identified: pre-dispersal (n = 7), dispersal (n = 8), and post-dispersal/residency (n = 14). Positions are shown in geographical coordinate system.

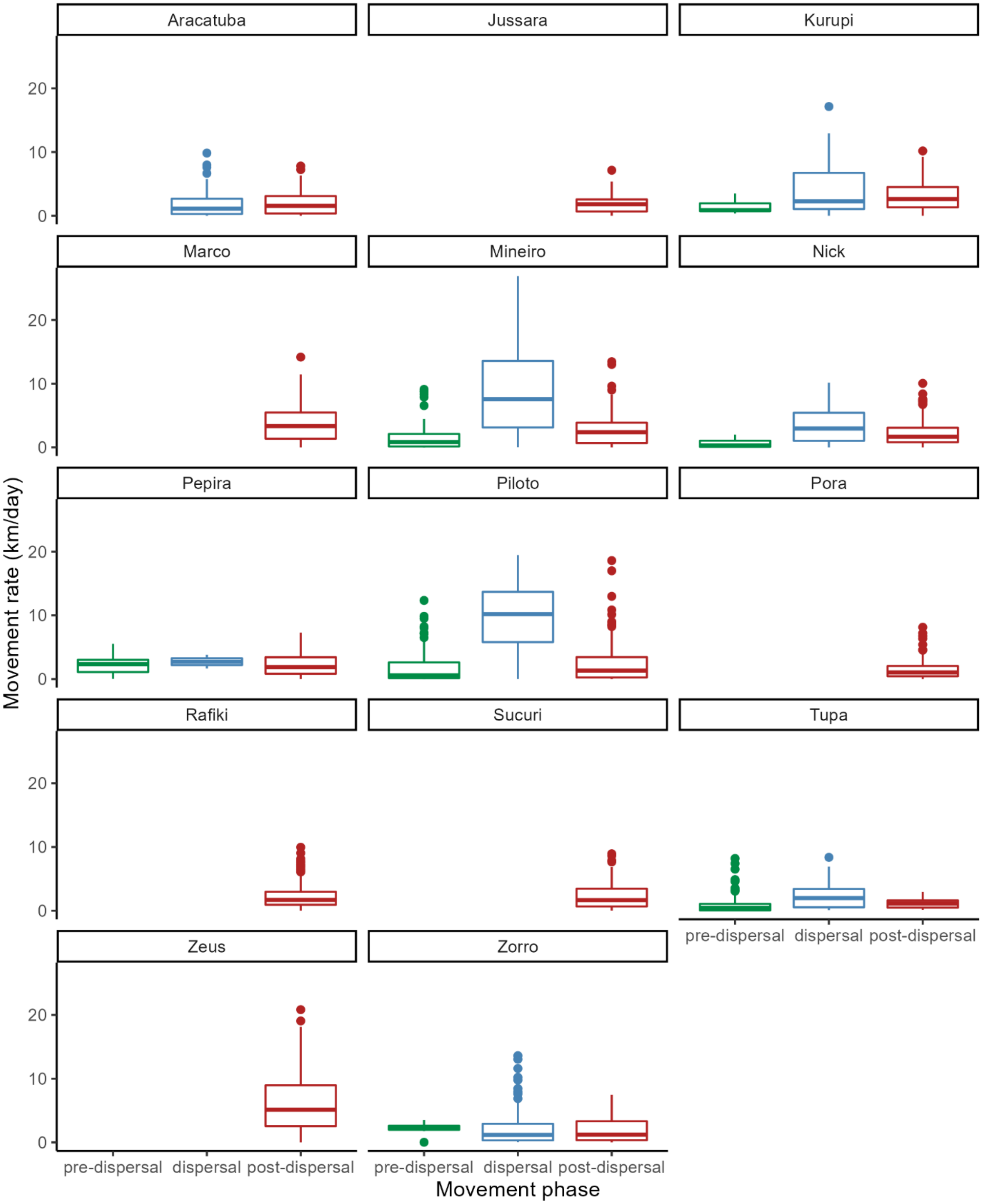

Figure D2. Median, first and third quartiles, and extreme values of the daily movement rate of each individual during each movement phase. The movement rate is based on a single average position per day for each puma. In general, movement rates were higher during dispersal than before or after dispersal, and higher in post-dispersal than in pre-dispersal phase. However, these differences varied among individuals.

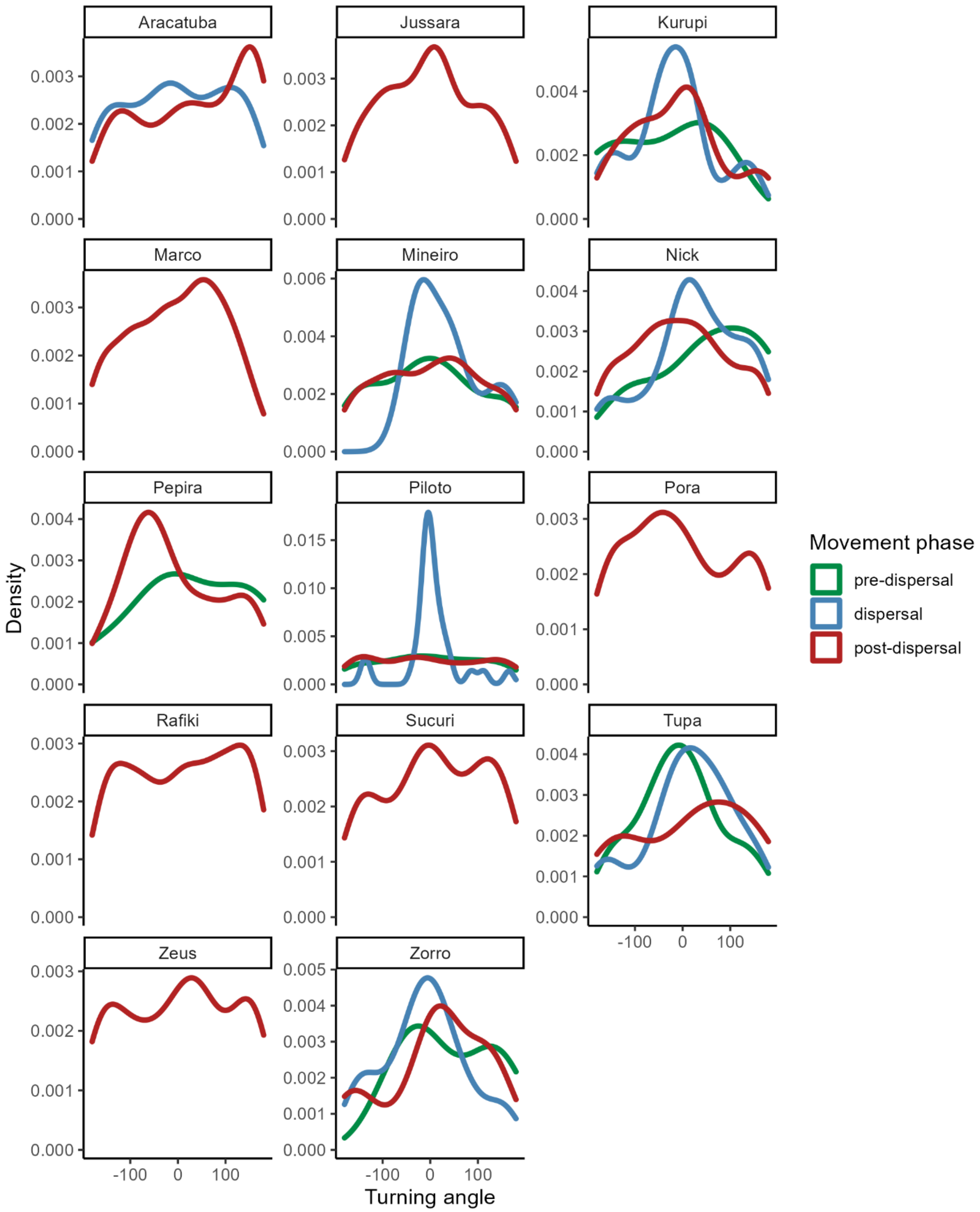

Figure D3. Distribution of turning angles of the movement of each individual during each movement phase. The turning angles is based on a single average position per day for each puma. In general, turning angles were more concentrated around zero (high directional persistence) during dispersal than before or after dispersal, even though this was not consistent across all individuals.

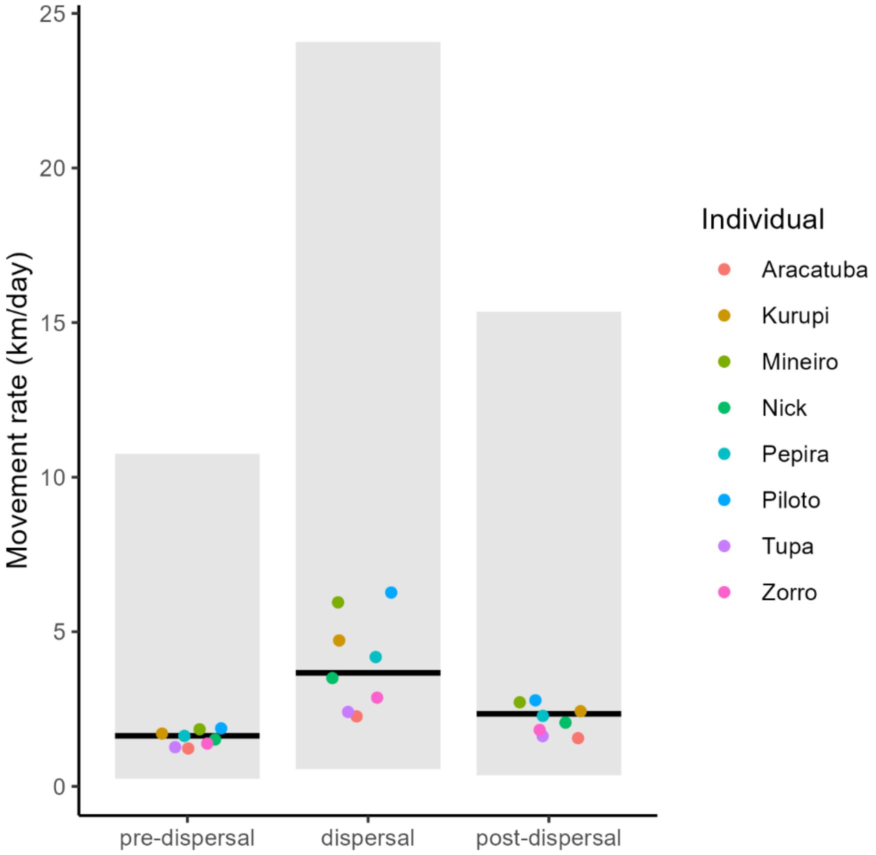

Figure D4. Expected daily movement rate predicted for all the dispersers (mean represented by the black line, 95% CI by the grey rectangle) and for each individual disperser separately (colored dots), using a generalized linear mixed model (see *Methods* in the main text). In general, movement rates were higher during dispersal then in post- and pre-dispersal movement phases.

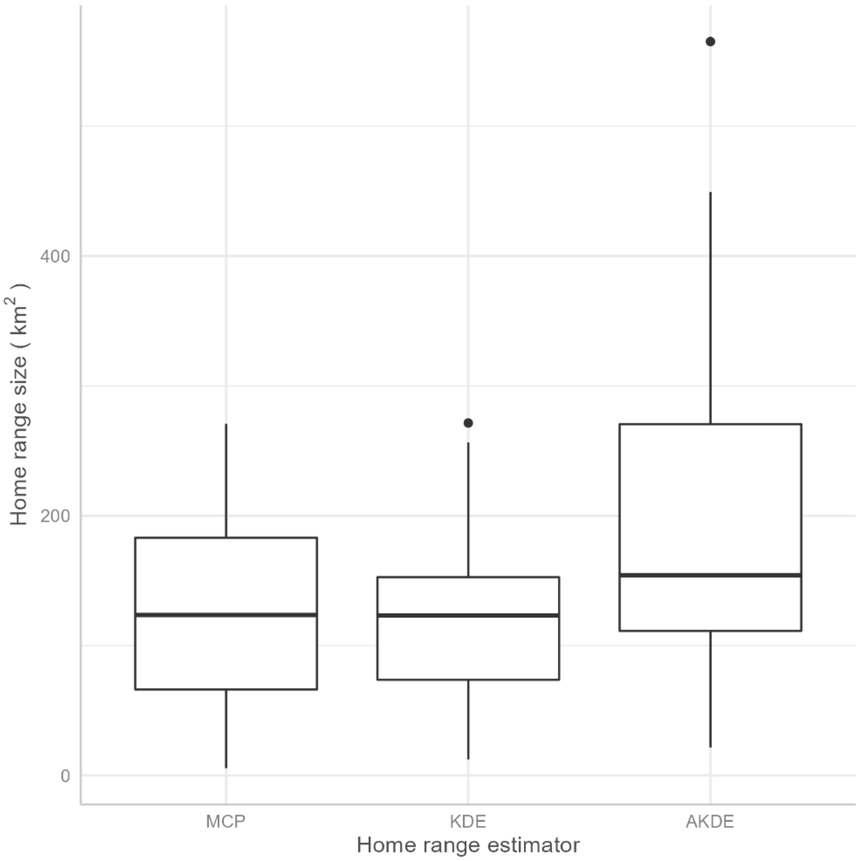

Figure D5. Boxplot of home ranges sizes of pumas estimated through different estimators. MCP = minimum convex polygon, KDE = kernel density estimation, AKDE = autocorrelated kernel density estimation. As expected, the estimates from AKDE are wider than those with MCP and KDE.

Figure D6. Proportion of puma GPS locations in different land use types, for dispersal and residency phases, during day and night, for each individual separately. Other anthropogenic uses consist of agricultural areas (mainly citrus and small areas of coffee or other crops) as well as low productive pastures and bare soil.

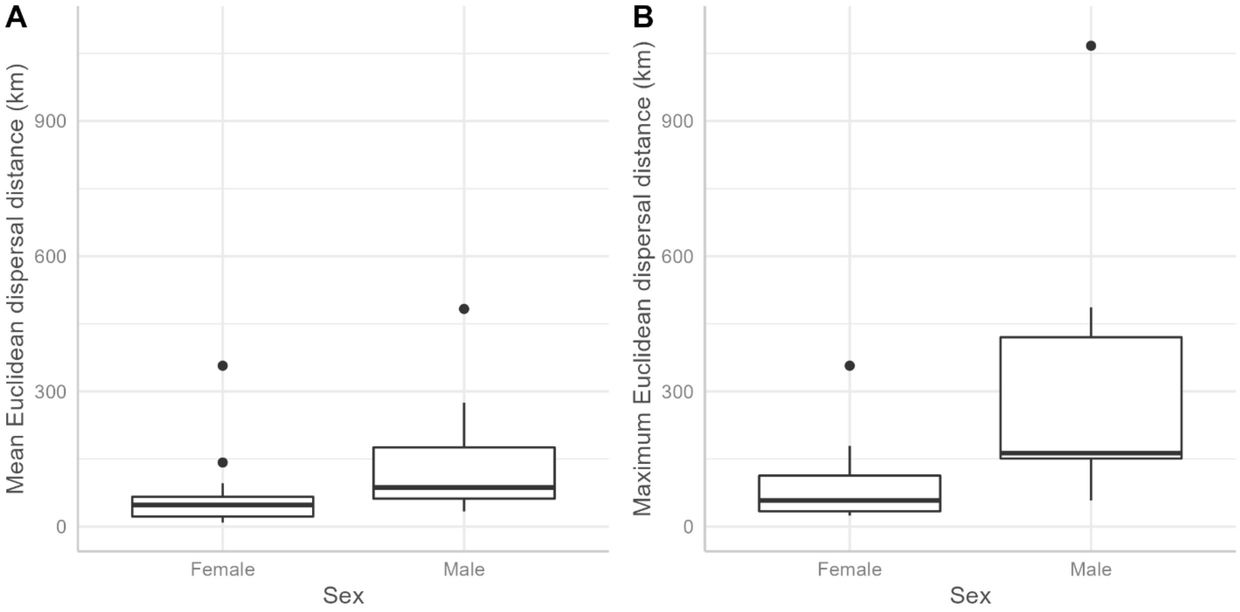

Figure D7. Boxplot of the (A) mean and (B) maximum Euclidean dispersal distance of pumas for females and males.

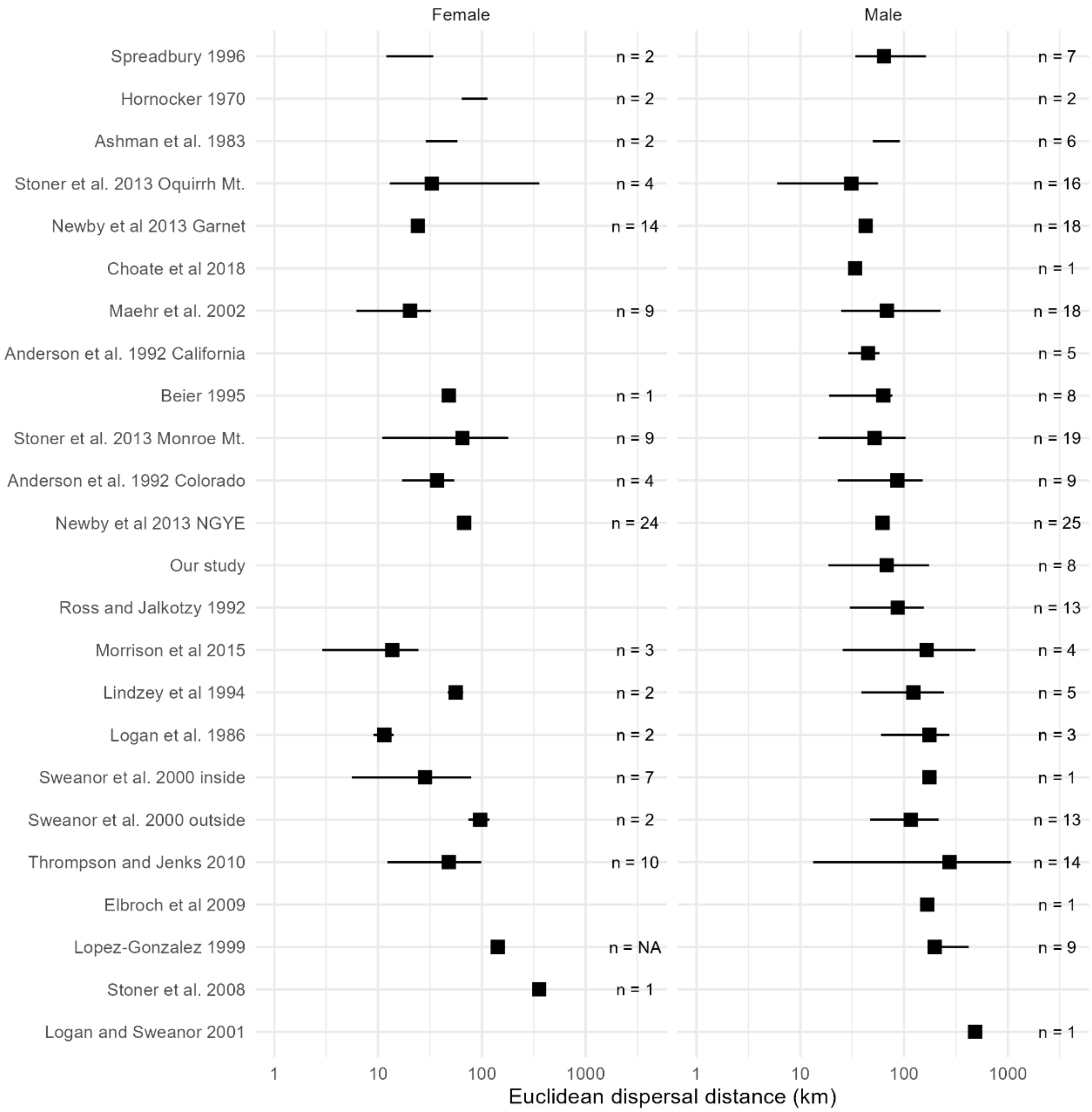

Figure D8. Forest plot of Euclidean dispersal distances by female (left panel) and male (right panel) pumas, showing the average (square) and range of dispersal distances (extremes of the line). Average, minimum, and maximum values were marked if reported by the studies. The number of individuals is shown at the right of each estimate. The *x* axis is presented in log10 scale to ease visualization; note, however, that it makes it harder to see long distance dispersal events. Check the histogram of dispersal distances in the original scale in Figure 6 of the main text for comparison. Some studies present more than one study area. Four studies were omitted from the figure: Hawley et al. (2016) reported a very long-distance dispersal event based on genetic analysis, > 2400km, is an outlier compared to the rest of the data and uses different (genetic) methods; Hemker et al. (1984) does not have individual sex associated with dispersal events; Weaver et al. (1996) presents only the maximum dispersal distance and Hornocker et al. (1970) presents only maximum dispersal distance for males – this data cannot be shown in forest plots.

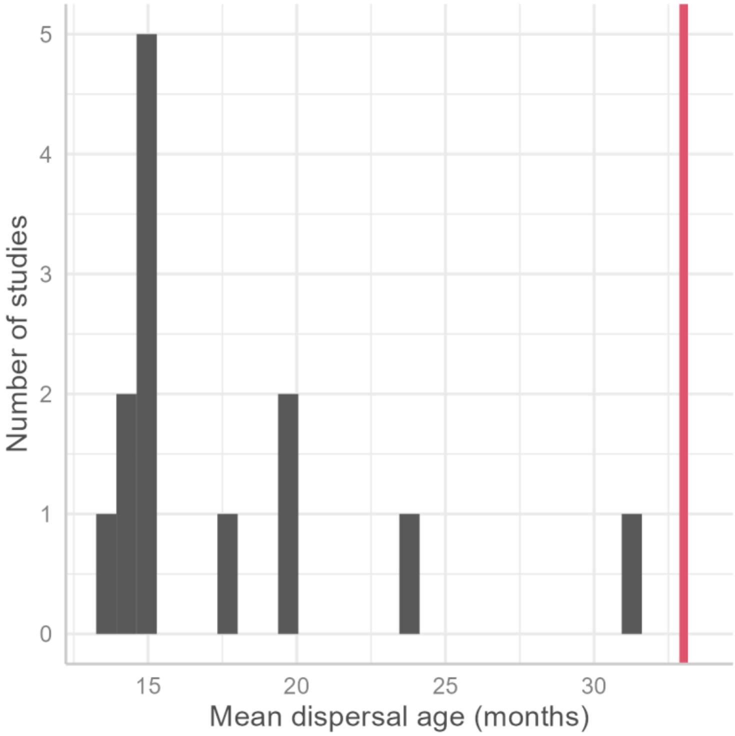

Figure D9. Mean dispersal age reported in the literature (grey bars) and by our study with pumas in Southeastern Brazil (red line). The discrepancy in the reported values might be related to the fact that the individuals monitored in our study were not tracked from their natal ranges.

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